Data gathering and input parameters to construct ecosystem models for the northern Gulf of St. Lawrence (mid-1980s)

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2003

Canadian Technical Report of
Fisheries and Aquatic Sciences 2497

Canadian Technical Report of Fisheries and Aquatic Sciences

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104-00675/

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Cat. No. Fs 97–6/2497E ISSN 0706–6457

Correct citation for this publication:

Morissette, L., S.-P. Despatie, C. Savenkoff, M. O. Hammill, H. Bourdages, and D. Chabot. 2003. Data gathering and input parameters to construct ecosystem models for the northern Gulf of St. Lawrence (mid-1980s). Can. Tech. Rep. Fish. Aquat. Sci. 2497: vi+94 p.

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ABSTRACT / RÉSUMÉ

Morissette, L., S.-P. Despatie, C. Savenkoff, M. O. Hammill, H. Bourdages, and D. Chabot. 2003. Data gathering and input parameters to construct ecosystem models for the northern Gulf of St. Lawrence (mid-1980s). Can. Tech. Rep. Fish. Aquat. Sci. 2497: vi+94 p.

In the present study, we use Ecopath and inverse methods to reconstruct trophic flows through the whole northern Gulf of St. Lawrence ecosystem (NAFO zones 4RS) for the mid-1980s period, prior to the groundfish stock collapses. This was a period of relatively constant biomass for the major species. The whole-system model of the northern Gulf of St. Lawrence is divided into 32 functional groups or compartments from phytoplankton and detritus to marine mammals and seabirds, including harvested species of pelagic, demersal, and benthic domains. We present here details of the input data (biomass, production, consumption, export, and diet composition) for each compartment used for modelling. The successful development of ecosystem models proposed by the Comparative Dynamics of Exploited Ecosystems in the Northwest Atlantic (CDEENA) program will provide powerful new tools to evaluate the impact of human and environmental factors on a variety of Atlantic shelf ecosystems.

RÉSUMÉ

Morissette, L., S.-P. Despatie, C. Savenkoff, M. O. Hammill, H. Bourdages, and D. Chabot. 2003. Data gathering and input parameters to construct ecosystem models for the northern Gulf of St. Lawrence (mid-1980s). Can. Tech. Rep. Fish. Aquat. Sci. 2497: vi+94 p.

Dans cette étude, nous utilisons les méthodes Ecopath et inverses pour représenter les flux trophiques de l'écosystème complet du nord du Golfe du Saint-Laurent (divisions 4RS de l'OPANO) pour le milieu des années 1980, avant l'effondrement des stocks de poissons de fond. Les biomasses des principales espèces étaient relativement constantes pendant cette période. L'écosystème du nord du Golfe du Saint-Laurent a été divisé en 32 groupes ou compartiments trophiques depuis le phytoplancton et les détritus jusqu'aux oiseaux et mammifères marins incluant les espèces commerciales des domaines pélagique, démersal et benthique. Nous présentons ici le détail des données (biomasse, production, consommation, export et composition alimentaire) pour chaque groupe utilisé pour les modélisations. Le succès de l'élaboration des modèles écosystémiques proposés par le programme « Comparative Dynamics of Exploited Ecosystems in the Northwest Atlantic » (CDEENA) apportera de nouveaux outils scientifiques efficaces pour évaluer l'impact des facteurs humains et environnementaux dans différents écosystèmes côtiers de l'Atlantique.

PREFACE

This work was supported by a multidisciplinary and inter-regional program known as CDEENA (Comparative Dynamics of Exploited Ecosystems in the Northwest Atlantic). CDEENA originally proposed a comparative analysis of changes in the structure and function of northwest Atlantic shelf ecosystems to determine how these may have affected the productivity of living resources. To this end, CDEENA brought together the expertise of field scientists and modellers to: (1) describe the changes in time and space, (2) identify and fill critical data gaps in the knowledge base, and (3) develop models to investigate ecosystem-level hypotheses (i.e., environmental variation, predation, fishing effects) concerning changes in reproduction, mortality, growth, and feeding of cod and other species.

The ecosystems that will be studied are the Newfoundland Shelf (NAFO 2J3KLNO), the northern Gulf of St. Lawrence (NAFO 4RS), the southern Gulf of St. Lawrence (NAFO 4T), the eastern Scotian Shelf (NAFO 4VsW), and the western Scotian Shelf (NAFO 4X). CDEENA focuses on three periods: (1) the 1970s, prior to the extension of the Canadian jurisdiction on fisheries to 200 miles (1977) and the subsequent recovery of some groundfish stocks in some of these areas; (2) the mid-1980s, the peak of the recovery and prior to the groundfish collapses of the early 1990s in virtually all areas; and (3) the mid-1990s, when the collapsed groundfish stocks have failed to recover in most areas. Due to the lack of data, the 1970 period was not investigated in the northern Gulf. The program will test the hypothesis that the failure of the collapsed fish stocks to recover in the 1990s is explained by changes in the ecosystems of the NW Atlantic (e.g., changes in trophic structure) driven by a combination of biological, fishing, and environmental variation that affected the recruitment of young stages, either through predation or competition for resources.

INTRODUCTION

During the early 1990s, groundfish stocks in Atlantic Canada collapsed, resulting in a moratorium on fishing of many stocks throughout eastern Canada. In the northern Gulf of St. Lawrence, the collapse of the cod fishery was attributed to a combination of environmental changes that led to a reduction in recruitment and an increase in natural mortality combined with over-exploitation (Dutil et al. 1998). Like other Atlantic cod stocks, the northern Gulf of St. Lawrence stock shows limited signs of recovery for reasons that are not understood (Fréchet and Schwab 1998).

Traditional studies on Atlantic cod stocks have followed a single species approach, where abundance has been evaluated using Virtual Population Analysis (VPA), incorporating catch data from the commercial fishery and research vessel surveys. In recent years, some attempts have been made to incorporate some ecosystem factors such as predation into the VPA analysis (Mohn and Bowen 1996; Fu et al. 2001), but this approach has been limited to single predator effects. Generally, the single species approach ignores the multiple effects of external factors such as prey abundance, predation, or competition from other components in the ecosystem. Owing to the widespread nature of the Atlantic cod fishery collapse and failure to recover, it is evident that a larger all-encompassing approach is needed to understand whether all of the cod stocks are affected in a similar way. Consequently, Fisheries and Oceans Canada developed a multi-year research program entitled "Comparative Dynamics of Exploited Ecosystems of the Northwest Atlantic" (CDEENA) to examine changes that might have occurred in the northwest Atlantic ecosystems over the last three decades. The objective was to develop individual ecosystem models for the northern Gulf of St. Lawrence (Northwest Atlantic Fishing Organization [NAFO] zones 4RS), southern Gulf of St. Lawrence (NAFO zone 4T), the Newfoundland and Labrador coast and offshore region (NAFO zones 2J3KLNO), and the Scotian Shelf region off the coast of Nova Scotia (NAFO zones 4VsWX) just prior to the groundfish collapses of the early 1990s in virtually all areas (mid-1980s) and the present (mid-1990s), when the collapsed groundfish stocks have failed to recover (Figure 1).

Here we present data gathering and input parameters used to construct inverse and Ecopath models of the northern Gulf of St. Lawrence ecosystem (NAFO zones 4RS) during the pre-collapse (1985–1987) period.

MATERIAL AND METHODS

Model structure

Under the steady-state assumption, consumption, representing the input, must balance the sum of the outputs consisting of, e.g., production, respiration, and egestion (non-assimilated food or detrital flow) for individual compartments. Consumption represented ingestion of prey both within and outside the system (i.e., import).

$$\text{Consumption} = \text{production} + \text{egestion} + \text{respiration} \tag{1}$$

Production of a given group included biomass accumulation as well as the biomass lost to natural mortality (predation, disease, and other natural causes of death) and export. Export from a group consisted of catches (fishing mortality) and net migration (migration out of or into the study area, food intake of predators that are not part of the system, etc.).

Production = biomass accumulation + predation + other mortality + export (2)

Assuming that there were no year-to-year changes in biomass over the 1985–1987 time period and that net migration was zero, production was simply the biomass lost to predation, natural mortality other than predation, and fishing mortality. Finally, the general mass-balance equation for individual compartments can be written as:

Consumption - egestion - respiration - predation - other mortality - fishing mortality = $0 + \varepsilon$ (3)

The equations calculated for this study were not "absolutely" balanced, that is, the sum of the inputs and outputs for each compartment did not necessarily equal zero and the specified local values (data equations) were not reproduced exactly. These differences are here termed the residuals which are represented by the error term ε.

For the phytoplankton group, the net (corrected for respiration) production must balance the sum of the outputs (phytoplankton mortality including the egestion term and consumption of phytoplankton). For the detritus group, the inputs (egestion and other natural causes of death for other groups) must balance the sum of the outputs (consumption of detritus, bacterial remineralization of detritus, and burial). As bacteria were considered part of the detritus, detritus are assumed to respire.

Under the CDEENA program, mass-balance models using Ecopath (Christensen and Pauly 1993; Christensen 1995; Bundy et al. 2000) and inverse methodology (Vézina and Platt 1988; Savenkoff et al. 2001) have been constructed for different ecosystems in Atlantic Canada and for different time periods. These models, as opposed to traditional approaches, consider the ecosystem as a whole rather than its components separately and they provide a description of trophic interactions between all functional groups of the ecosystem. The models generate a "snapshot" of the system at one moment in time and use mass-balance principles to estimate flows of organic matter or energy among components of an ecosystem.

Ecopath with Ecosim (www.ecopath.org) is a widely used software to synthesize biomass and energetic data and to develop flow networks. The Ecopath modelling approach enables a description of the possible scenarios of relationships, flows, and interactions based on the known conditions in an ecosystem during a particular time period (Okey and Pauly 1999). It is based on an approach initially developed by Polivina (1984) to estimate biomass and food consumption of the different elements of an aquatic ecosystem. It has subsequently been combined with various approaches from theoretical ecology (Ulanowicz 1986) for the analysis of flows between ecosystem components (Christensen and Pauly 1992a).

Each group is represented by one balanced equation and requires six input parameters: biomass (B), production (P), consumption (Q), ecotrophic efficiency (EE; the fraction of the production that is either passed up the food web or exported), diet composition, and catch of each group (here equal to export). The linear equations are solved via matrix algebra to produce estimates of the flows that balance inputs and outputs; any missing parameters are estimated (EE is estimated if all parameters have been entered). Export and diet composition must always be entered while three of the four remaining basic input parameters (B, P, Q, and EE) must be entered. In most cases, when all the information to run an Ecopath model is assembled, the model will not balance due to the inconsistencies in the information. In this case, the values of one or more of the terms can be changed iteratively until a balance is obtained. Indeed, there is more than one way to construct a Ecopath model and there is no unique solution to any model. However, where there are areas of the model that are well known and on which the modeller can place some certainty, then the number of plausible solutions is reduced. For the less certain parameters, sensitivity analysis can be used to examine their effects on the model. The ecotrophic efficiency provides an immediate check for mass balance (Christensen and Pauly 1992a). If the model is not balanced, then there are negative flows to the detritus and ecotrophic efficiencies (EE) are greater than one. Arriving at a balanced network with the Ecopath approach is left largely to trial and error, either through user intervention or Monte-Carlo simulations.

Also, due to the fact that the ecosystem-level information is never complete (underdetermined system), Ecopath flow network solutions are not unique. We therefore need to use different approaches to the same data to ascertain the robustness of estimated flow networks. The inverse approach solves flow networks by finding the solution that minimizes the imbalances between inputs and outputs (Vézina and Platt 1988; Vézina et al. 2000; Savenkoff et al. 2001). Trophic flows are estimated using an objective least-squares criterion and the solution process generates the simplest flow network that satisfies both the mass conservation and constraints; e.g., the simplest solution in the sense of minimizing both the sum of squared flows (thus the total sum of flows through the food web) and the sum of squared residual errors. The mass balance is closed by residuals (inputs – outputs) instead of adding a new parameter such as "ecotrophic efficiency," as in the Ecopath approach.

The general structure of an inverse model includes: (1) compartmental mass-balance equations, (2) data equations, and (3) constraints. The data equations attempt to fix the value of certain flows or combination of flows (e.g., incorporate the observations into the model that coincide with the period/region for which a solution was tested) while the constraints incorporate general knowledge into the model. The input data introduced directly into the model as data equations included values for exports (catches) from the system, production, and diet proportions locally estimated from field studies or available only as point estimates (no variance estimate) or with low variance. The system of equations above was strongly underdetermined, so additional constraints (other conditions that reflect our prior knowledge of this system) were added to obtain a meaningful solution. Each flow was taken to be non-negative and the flows and ratios of flows (metabolic efficiencies) were assumed to fall within certain ranges to satisfy basic metabolic requirements. Gross growth efficiency (GE) is the ratio of production to consumption and for most groups should have values between 10 and 30% (Christensen and Pauly 1992b). Exceptions are top predators, e.g., marine mammals and seabirds, which can have lower GE (between 0.1 and 1%), and small, fast growing fish larvae or nauplii or bacteria, which can have higher GE (between 25 and 50%) (Christensen and Pauly 1992b). Following Winberg (1956), 80% of the consumption was assumed to be physiologically useful for carnivorous fish groups while the non-assimilated food (20%, consisting of urine and feces) was directed to the detritus. For herbivores, the proportion not assimilated could be considerably higher, e.g., up to 40% in zooplankton (Christensen and Pauly 1992b). We constrained the assimilation efficiency (AE) to fall between 70 and 90% for all groups except for large and small zooplankton (between 50 and 90%).

Certain flows have a minimal and maximal value imposed (export for detritus, production, consumption, diet composition, etc.). The production and consumption values that were not estimated from local field studies were incorporated as constraints. Diets with reasonable estimates of uncertainty (SD greater than 0.6%) were also specified as constraints. To facilitate comparisons with other mass-balance models found in the literature (e.g., Ecopath models), we added constraints on the ecotrophic efficiency (EE). The ecotrophic efficiency is the fraction of the production that is either passed up the food web or exported. These values should be between 0 and 0.95 (Christensen and Pauly 1992b, 1998). Here, a value only slightly above zero indicates that the group is not consumed in noticeable amounts by any other group in the system (e.g., top predators). Conversely, a value near or equal to 0.95 indicates that the group is heavily preyed upon and/or highly exploited by a fishery, leaving no individuals to die of other causes (small prey organisms).

Study area

The Gulf of St. Lawrence is a 200,000 km^2 semi-enclosed sea that empties into the Atlantic Ocean via Cabot Strait in the south and the Strait of Belle-Isle in the north (Dunbar et al. 1980). The Gulf of St. Lawrence is supplied at the same time by relatively warm Atlantic water entering via Cabot Strait (Lauzier and Trites 1958) and by cold Labrador Current water entering through the Strait of Belle-Isle (Koutitonsky and Bugden 1991). There is also a large amount of freshwater that enters from the St. Lawrence River and other large rivers along the New Brunswick coast and the Québec north shore. Almost half of its area is occupied by deep channels, notably the Laurentian Channel, which extends nearly 1,000 km from the St. Lawrence Estuary to the Atlantic Ocean, and the Esquiman and Anticosti channels (Figure 1). The official sampling area used in our models for the calculation of densities represented the surface of strata sampled for the northern Gulf of St. Lawrence survey. These strata were all deeper than 37 meters, so it excluded the shallow water zone, and covered a total area of 103,812 km^2.

The northern Gulf of St. Lawrence ecosystem is characterized by phytoplankton consisting mainly of large diatoms during the spring bloom and small flagellates in summer, a low diversity of large zooplankton species (euphausiids, chaetognaths, amphipods, and shrimp), a relatively low-abundance fish community dominated by cod, herring, and redfish (*Sebastes* sp.), and a high abundance of juvenile fish (primarily capelin [*Mallotus villosus*]) (de Lafontaine et al. 1991).

Functional groups

Functional groups were based on individual species of commercial significance as predator or prey (and occasionally on size/age of these species; see below) or groupings of ecologically or taxonomically related species. We distinguished five marine mammal groups, one seabird group, sixteen fish groups, eight invertebrate groups, one phytoplankton group, and one detritus group. Some groups such as large pelagic feeders and large demersal feeders are aggregated groups, where the species were grouped on the basis of similarity of size and ecological role (Table 1). The input parameters of these groups should simply be the means of the component parameters weighted by the relative biomass of the components (Christensen et al. 2000).

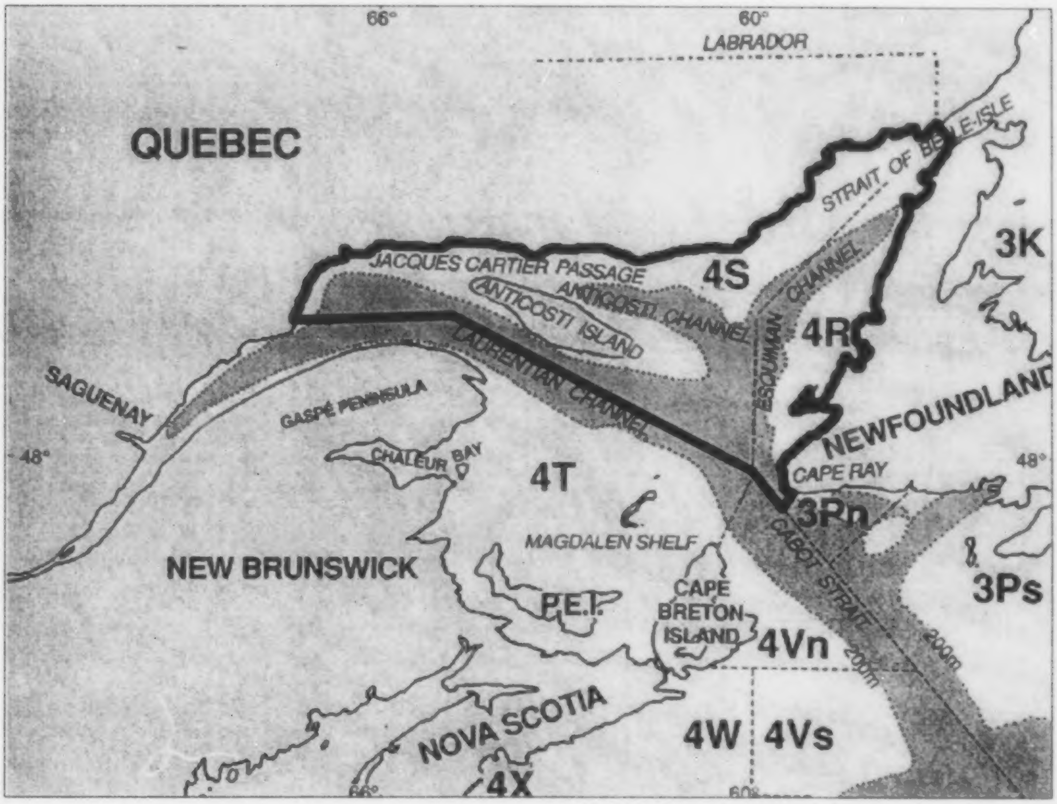
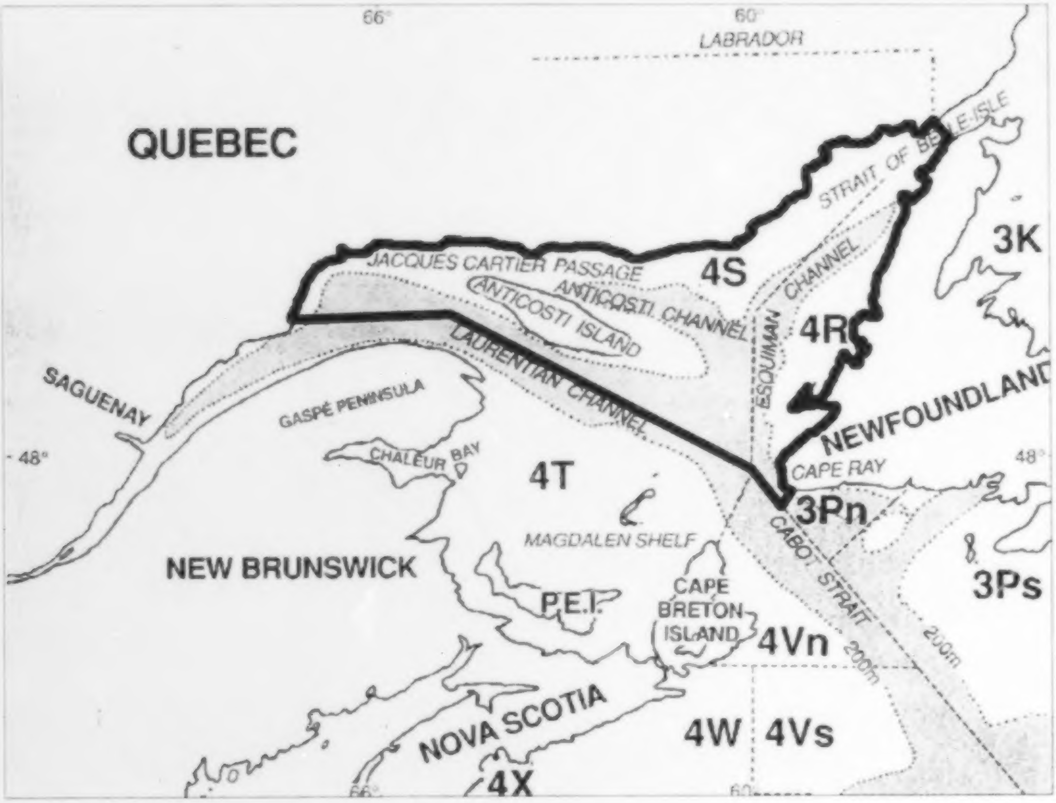

66°
60°
LABRADOR
QUEBEC
STRAIT OF BELLE-ISLE
3K
JACQUES CARTIER PASSAGE
4S
ANTICOSTI ISLAND
ANTICOSTI CHANNEL
ESQUIMAN CHANNEL
4R
LAURENTIAN CHANNEL
SAGUENAY
GASPÉ PENINSULA
NEWFOUNDLAND
48°
CHALEUR BAY
4T
CAPE RAY
48°
3Pn
MAGDALEN SHELF
CABOT STRAIT
NEW BRUNSWICK
3Ps
CAPE BRETON ISLAND
P.E.I.
4Vn
200m
200m
NOVA SCOTIA
4W
4Vs
4X
66°
60°

Figure 1. The Gulf of St. Lawrence (modified from Therriault 1991).

Atlantic cod and Greenland halibut were each separated into two groups based on diet composition, age/size at first capture, and age/size at maturity. Smaller animals prey mainly on invertebrates while larger animals prey mainly on fish (Bundy et al. 2000). In fact, an isotopic shift in carbon signatures occurs around 40 cm for Greenland halibut; a similar shift can be observed at a length of 35 cm for the nitrogen signature of Atlantic cod (Lesage et al. 2001).

Collecting the data

All the parameter estimations were made within a collaborative approach, in which experts for the various components were consulted. A considerable effort has been expended to obtain input data in the study area and during the period of interest. However, information on several groups (e.g., forage species, benthic invertebrates, and zooplankton) was sparse or non-existent for the area and period studied and was thus taken from the literature or for the same area but another time period (mid to late 1990s). These different sources of data (local and literature) explain the high coefficients of variation for the production, consumption, and diet data (93, 64, and 119%, respectively) compared with those of biomass or export (66 and 46%, respectively).


66°
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LABRADOR
QUEBEC
STRAIT OF BELLE ISLE
3K
JACQUES CARTIER PASSAGE
4S
ANTICOSTI CHANNEL
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ESQUIMAN CHANNEL
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48°
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200m
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4W
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Biomass

The biomass density (called biomass in this document) of a species (or group of species) was assumed to be constant for the 1985–1987 period covered by the model. The biomass of each box of the model was obtained directly or was estimated from similar ecosystems when it was not available for 4RS. This parameter is expressed in biomass per surface unit (e.g., tons wet weight km^{-2}) (Christensen and Pauly 1993). Biomass was estimated from sequential population analysis or scientific trawl survey data for most groups in the model.

An annual trawl survey for groundfish was conducted between 1984 and 1990 in the northern Gulf aboard the CCGS *Lady Hammond*. The sampling strategy used consisted of a stratified random sampling following predetermined strata based on depth (Doubleday 1981). Stratified random means were calculated to estimate the biomass in the area using the *PACES* (*Programme d'Analyse des Campagnes d'Échantillonnage Stratifiés*) software (Bourdages 2001).

The use of trawl data to estimate biomass of fish species involves inherent problems due to variable catchability of the different species considered. Different species have different degrees of catchability by the fishing gear, making comparison of biomass estimates difficult at best. Trawlable biomass estimates were thus converted to catchability-adjusted biomass based on catchability coefficients estimated by Harley and Myers (2001). Length-specific corrections were applied to numbers-at-length data before they were converted to biomass estimates. In this way, we hoped to lessen the impact of catchability on the biomass estimates and render data comparable between species.

To estimate the biomass of younger age classes not captured in the survey, numbers-at-age were back-calculated from a known number of the first year class captured in the survey, assuming a natural mortality rate, and then multiplying by mean mass-at-age to get mean biomass-at-age.

Production

Production is the total amount of tissue produced in the population or community under study during a given time period (Christensen and Pauly 1992a). It includes all living matter produced by a group (even if it's finally consumed, fished, or lost by other mortality) during the model period (Christensen and Pauly 1992b). Total mortality (Z), under the steady-state assumption, is equal to the production/biomass ratio (P/B) (Allen 1971; Pauly 1997).

Measurement of this production over the target time period requires information on the population's biomass at the beginning and the end of the period and the mass of living components that have been lost by death or emigration (Bundy et al. 2000). In the northern Gulf of St. Lawrence model, it is assumed that there is no year-to-year change in biomass over the 1985–87 time period and that emigration is zero. Thus production in this model is simply the biomass that is lost to natural mortality (predation, disease, and other natural causes of death) and fishing mortality. Absolute production is a flux expressed in biomass per surface unit per year (e.g., $t\ km^{-2}\ yr^{-1}$).

Table 1. Functional groups used in modelling for the 1985–1987 period in the northern Gulf of St. Lawrence.

Group Name	Main species
Cetaceans	*Balaenoptera physalus*, *Balaenoptera acutorostrata*, *Lagenorhynchus acutus*, *Lagenorhynchus albirostris*, *Megaptera novaeangliae*, *Phocoena phocoena*
Harp seals	*Phoca groenlandica*
Hooded seals	*Cystophora cristata*
Grey seals	*Halichoerus grypus*
Harbour seals	*Phoca vitulina*
Seabirds	*Alca torda*, *Cepphus grylle*, *Fratercula arctica*, *Larus argentatus*, *L. delwarensis*, *L. marinus*, *Morus bassanus*, *Oceanodroma leucorhoa*, *Phalacrocorax auritus*, *P. carbo*, *Sterna hirundo*, *S. paradisaea*, *Rissa tridactyla*, *Uria aalge*
Large Atlantic cod (> 35 cm)	*Gadus morhua*
Small Atlantic cod (≤ 35 cm)	*Gadus morhua*
Large Greenland halibut (> 40 cm)	*Reinhardtius hippoglossoides*
Small Greenland halibut (≤ 40 cm)	*Reinhardtius hippoglossoides*
American plaice	*Hippoglossoides platessoides*
Flounders	*Glyptocephalus cynoglossus*, *Limanda ferruginea*, *Paralichthys oblongus*, *Pseudopleureonectes americanus*
Skates	*Raja laevis*, *R. ocellata*, *R. radiata*, *R. senta*, *R. spinicauda*,
Redfish	*Sebastes fasciatus*, *S. mentella*
Large demersal feeders	*Anarhichas* spp., *Centroscyllium fabricii*, *Cyclopterus lumpus*, *Hippoglossus hippoglossus*, *Lophius americanus*, *Melanogrammus aegelfinnus*, *Urophycis tenuis*, *Lycodes* spp., Macrouridae, Zoarcidae
Small demersal feeders	*Argentina* spp., *Emicrotremus* spp., *Macrozoarces americanus*, *Myoxocephalus* spp., *Tautogolabrus adspersus*, Bleniidae, Cottidae, Phjolidae, Zoarcidae, juvenile large demersal feeders
Capelin	*Mallotus villosus*
Sand lance	*Ammodytes americanus*, *A. dubius*
Arctic cod	*Boreogadus saida*

Table 1. Cont.

Group Name	Main species
Large pelagic feeders	*Cetorhinus maximus*, *Merluccius bilinearis*, *Pollachius virens*, *Squalus acanthias*, *Thunnus thynnus*
Piscivorous small pelagic feeders	*Illex illecebrosus*, *Scomber scombrus*, piscivorous myctophids and other mesopelagics, piscivorous juvenile large pelagic feeders
Planktivorous small pelagic feeders	*Clupea harengus harengus*, *Gonatus* spp., *Scomberesox saurus*, planktivorous myctophids and other mesopelagics, planktivorous juvenile large pelagic feeders
Shrimp	*Pandalus borealis*, *Pandalus montagui*
Large crustaceans	*Chionoecetes opilio*, other non-commercial species (*Hyas* spp.)
Echinoderms	*Echinarachnius parma*, *Ophiura robusta*, *Stronglyocentrotus pallidus*
Molluscs	*Cyrtodaria siliqua*, *Mesodesma deauratum*
Polychaetes	*Exogene hebes*
Other benthic invertebrates	Miscellaneous crustaceans, nematodes, other meiofauna
Large zooplankton (> 5 mm)	Euphausiids, chaetognaths, hyperiid amphipods, cnidarians and ctenophores (jellyfish), mysids, tunicates >5 mm, ichthyoplankton
Small zooplankton (< 5 mm)	Copepods (mainly *Calanus finmarchicus*, *C. hyperboreus*, and *Oithona similis*), tunicates < 5 mm, meroplankton
Phytoplankton	Diatom species such as *Chaetoceros affinis*, *Chaetoceros* spp., *Fragilariopsis oceanica*, *F. cylindrus*, *Leptocylindrus minimus*, *Thalassiiosira bioculata*, T. *nordenskioldii*, *T. pacifica*, *T. punctigera*, and a mixture of autotrophic and mixotrophic organisms including: Cryptophytes, dinoflagellates, Prasinophytes, Prymnesiophytes, and mixotrophic *Stombidium* spp.,
Detritus	

Consumption

Consumption is defined as the utilization of food by a group during the time period considered by the model (Christensen and Pauly 1993). Q/B is the ratio of consumption (Q) to biomass unit (B). Absolute consumption is a flux expressed in biomass per surface unit per year (e.g., t km^{-2} yr^{-1}).

Consumption was estimated from field studies where possible, either from the region or for species from similar areas reported in the literature. In addition, models were used to estimate consumption by marine mammals (Hammill and Stenson 2000) and seabirds (G. Chapdelaine, Environment Canada, Migratory Birds Division, Sainte-Foy, Québec, unpublished data).

Where it was not possible to do either, Q/B values were taken either from the literature and/or estimated assuming a gross growth efficiency (GE; the ratio of production to consumption) between 10 and 30% (Christensen and Pauly 1992b).

Diet composition

Diet matrices were constructed from field data from the study area whenever possible. However, these data do not exist for some species in the study area. For these species, diet data were obtained from literature reports for species in the area or for species from similar areas. If no data were available for the right period and the right area, we initially used data from the same area but from another period, and then data from the same period but from another area (giving priority to the areas that are more similar to the northern Gulf of St. Lawrence ecosystem). If nothing else was available, we used data from another area and another period of time. Based on these different sources of the data (local and literature), we estimated the lower and upper limits of each diet proportion used as inputs in inverse modelling. The means and standard deviations were calculated either directly from the lower and upper limits when there was no information on the number of stomachs or from the different diet proportions, which were weighted by the number of stomachs when stomach content analyses were given. The diet outputs estimated by the balanced (optimized) solution of inverse modelling were then used as inputs for the Ecopath model.

FishBase

Occasionally, information was not available for some parameters. When this happened we referred to FishBase (www.fishbase.org), which is a biological database developed at the International Centre for Living Aquatic Resources Management (ICLARM) in collaboration with FAO and other organizations. It includes information on more than 26,700 species of fish and is updated frequently with regards to information such as maximum size, growth parameters, natural mortality, and standardized diet composition (Froese and Pauly 1995). When no information was available from the literature for a particular species in the ecosystem, reference was made to this database.

Inverse modelling

Savenkoff et al. (2001) developed an inverse model equivalent to an Ecopath structure (Bundy et al. 2000) in the Newfoundland–Labrador Shelf for the 1985–1987 period, prior to the groundfish stock collapses. The solutions of the inverse and Ecopath models were compared to evaluate how much impact the solution method had on the construction of flow networks.

Differences between the solutions of the inverse and Ecopath models were much smaller than the range of solutions allowed by the inverse model constraints. In general, inverse estimates of efficiencies (growth efficiency, non-assimilated fraction, ecotrophic efficiency) were more dispersed than Ecopath efficiencies (non-assimilated fraction and ecotrophic efficiency often fixed at 20 and 95%, respectively, in the Ecopath solution), providing more flexibility to balance the flow networks. Moreover, the inverse method as applied here appeared to exploit the "breathing room" in transformation efficiencies to produce a more efficient system (catches/net primary production were 40% higher with the inverse solution than with the Ecopath solution), with lower total throughput and without changing the trophic structure significantly. The inverse model was useful to obtain a first balanced solution using an objective least-squares criterion.

In inverse modelling, different approaches (comparisons of different inverse networks, random perturbations, sensitivity tests, etc.) were applied to assess the solution's robustness to variations in the data and thus to provide an overall view of the ecosystem, to identify robust patterns, and to determine the location of uncertainties in the food web. To assess the solution's robustness to variations in the data, we applied random perturbations to input data. We randomly perturbed each element of the mass balance equations (data equations) by up to its standard deviation in order to represent the true uncertainties of the input data. Indeed, some of the input data were introduced as additional compartmental mass balance equations. These included values for exports (catches) out of the system, production, consumption, and diet proportions locally estimated from field studies or available only as point estimates (no variance estimate) or with low variance. All the local catch values (export) were used as data equations rather than treated them as constraints (e.g., the means were used rather than the upper and lower limits).

Finally, the final solution of inverse modelling was the mean of at least 31 balanced random perturbations (including a response without perturbation). The Ecopath model then used this final solution to estimate the biomass of each group corresponding to these inputs and important ecological indices (e.g., mean trophic level of the catches, trophic levels assigned to individual compartments, connectance, and omnivory). The Ecopath solution was also used in dynamic simulations between time periods with Ecopath with Ecosim software (Christensen et al. 2000).

RESULTS

In this section, each functional group of the northern Gulf of St. Lawrence ecosystem is described along with respective estimates of biomass, production, consumption, and diet composition that are used as inputs for modelling.

Cetacea

Background

The northern Gulf of St. Lawrence is dominated by boreal cetaceans ranging from large and medium-sized mysticetes and odontocetes to small odontocetes such as porpoises and dolphins (Kingsley and Reeves 1998). Minke (*Balaenoptera acutorostrata*), fin (*Balaenoptera physalus*), long-finned pilot (*Globicephala melas*), and humpback whales (*Megaptera novaeangliae*) are the most abundant species among the large and medium whales. The harbour porpoise (*Phocoena phocoena*) is the most abundant of the small dolphins in the Gulf while white-sided dolphins (*Lagenorhynchus acutus*) and white-beaked dolphins (*Lagenorhynchus albirostris*) also occur in this area (Kingsley and Reeves 1998). The cetacean survey of the Gulf of St. Lawrence (Kingsley and Reeves 1998) covered 244,792 km^2, so we used this inventory area to calculate the parameters for this group instead of the value habitually used for the other groups (the sampling area for zones 4RS).

Catch

Canada ceased commercial whaling in 1972 and there has been no hunt for subsistence purposes in 4RS. However, information from a questionnaire survey conducted in 1989 and 1990 in the Gulf 4RST indicated an annual average incidental catch from fishing gear of 1,835 harbour porpoises (Fontaine et al. 1994a). This is equivalent to a catch of 92 tons within a 244,792 km^2 sampling area ($3.75 \times 10^{-4} \pm 2.09 \times 10^{-5}$ t km^{-2} yr^{-1}). The final solution of inverse modelling (hereafter termed "inverse solution") estimated a catch of 3.74×10^{-4} t km^{-2} yr^{-1}.

Biomass

Aerial survey estimates of cetacean abundance in the Gulf of St. Lawrence, not corrected for visibility bias, are available for the summer of 1995 (Kingsley and Reeves 1998). The area of the strata corresponding to the northern Gulf covers 144,468 km^2, the density in this zone is applied to the present study zone. These estimates were adjusted by a factor of 1.09 to account for animals that were potentially visible to the observers but were not seen (Marsh and Sinclair 1989) and by a factor of 2.27 to account for animals missed owing to water turbidity (Marsh and Sinclair 1989). These adjustments resulted in mean abundance estimates of 169 humpback whales (back-calculated from a total of 297 in 1995 and a 6.5% growth rate [Barlow and Clapham 1997)]), 553 fin whales (back-calculated from a total of 990 in 1995 and a 6.7% growth rate [Bundy et al. 2000]), 1,189 minke whales (back-calculated from a total of 2,128 in 1995 and a 6.7% growth rate [Bundy et al. 2000]), 2,122 long-finned pilot whales (back-calculated from a total of 3019 in 1995 and a 4% growth rate [Waring et al. 1999]), 16,367 harbour porpoises (back-calculated from a total of 21,427 in 1995 and a 9% growth rate [Caswell et al. 1998] and added to an annual incidental catch of 1,083 individuals), 14,577 white-sided dolphins (back-calculated from a total of 17,419 in 1995 and a 2% growth rate [Heise 1997]), and 5,467 white-beaked dolphins (back-calculated from a total of 6,532 in 1995 and the 2% growth rate used for white-sided dolphins [Heise 1997]). Other whales, like blue whales for instance, were present in the survey of the Gulf of St. Lawrence but were seen too infrequently to allow any estimation of their biomass.

Mean body mass taken from the literature was 31 t for humpback whales (averaged from Hay [1985], Martin [1990], and Kenney et al. [1997]); 38.5 t for fin whales, 5.6 t for minke whales, 1.4 t for long-finned pilot whales, and 0.05 t for harbour porpoises (averaged from Lien [1985], Martin [1990], and Kenney et al. [1997]); 0.13 t for white-sided dolphins (Sergeant et al. 1980); and 0.217 t for white-beaked dolphins (Ridgway and Harrison 1999). Assuming a residence time of 180 days for all whales within the area covered by the survey of Kinglsley and Reeves (1998) (i.e., 144,468 km^2), the average annual biomass was 19,747 tons or 0.137 t km^{-2}.

Production

Because there is no information on total mortality for cetaceans, production is assumed to be equivalent to the biomass multiplied by natural mortality plus catch. Natural mortality for a combination of cetaceans was estimated to range between 0.074 (Tanaka 1990) and 0.075 (Ohsumi 1979), and the mean annual catch used was 92 tons (Fontaine et al. 1994a). This resulted in a total P/B of 0.077 yr^{-1} and a total annual production of 0.011 t km^{-2} yr^{-1}. Based on the annual consumption of Trites et al. (1997) (see below) and the upper GE limit (1%; values based on lower GE limit of 0.1% were not realistic), we obtained another production value: 0.008 t km^{-2} yr^{-1}. The mean production value was 0.010 ± 0.002 t km^{-2} yr^{-1}. The inverse solution estimated a production of 0.009 t km^{-2} yr^{-1}, representing a P/B of 0.066 yr^{-1}.

Consumption

The daily consumption by cetaceans was calculated using:

$$R = 0.1W^{0.8} \tag{4}$$

where R is the daily ration for an individual in kg and W is the mean body mass in kg (Trites et al. 1997). Assuming a residence time of 180 days, the annual mean consumption by species is 0.082 t km^{-2} yr^{-1} for humpback whales, 0.321 t km^{-2} yr^{-1} for fin whales, 0.148 t km^{-2} yr^{-1} for minke whales, 0.087 t km^{-2} yr^{-1} for long-finned pilot whales, 0.047 t km^{-2} yr^{-1} for harbour porpoises, 0.089 t km^{-2} yr^{-1} for white-sided dolphins, and 0.050 t km^{-2} yr^{-1} for white-beaked dolphins. This gives a mean annual consumption of 0.824 t km^{-2} yr^{-1}. Gross growth efficiency (GE = P/Q) ranges between 0.1 and 1% for marine mammals (Christensen and Pauly 1992b). Based on the previous total annual production (0.011 t km^{-2} yr^{-1}) and the GE limits, we obtained two other consumption values of 0.969 and 9.689 t km^{-2} yr^{-1}, respectively. The value based on the lower GE limit was not realistic, so we used the value based on the upper GE limit and the previously reported value to estimate a consumption range between 0.824 and 0.969 t km^{-2} yr^{-1}. The mean consumption values are 0.896 ± 0.102 t km^{-2} yr^{-1}. The inverse solution estimated a consumption of 0.960 t km^{-2} yr^{-1}, representing a Q/B of 7.024 yr^{-1}.

Diet composition

Unfortunately, there are few quantitative descriptions of diet for cetaceans. Where the literature refers to prey using terms such as "preponderant" or "predominant," it was assumed that they make up at least 75% of consumption by mass. If other prey were reported, remaining consumption was divided equally among them. Based on the literature, the following diets were used in the analysis:

- Humpback whales: capelin, sand lance, squid, and euphausiids (Mitchell 1973)
- Fin whales: capelin, sand lance, herring, and euphausiids (Mitchell 1975)
- Minke whales: capelin, small cod, herring, squid, and euphausiids (Horwood 1990)
- Long-finned pilot whale: squid, small cod, and capelin (Lien 1985)
- Harbour porpoises: capelin, herring, redfish, mackerel, cod, squid, and sand lance (Fontaine et al. 1994b)
- White-sided dolphins: herring (*Clupea harengus*), squid, smelt, silver hake, and crustaceans (Katona et al. 1978)
- White-beaked dolphins: cod, whiting, mackerel, and cephalopods (Santos et al. 1994).

For cetacean species, prey were assigned to the appropriate functional groups of the model and the importance of each group was calculated in % mass of total diet for each cetacean (Table 2). These contributions were then averaged across cetacean species and weighted according to each species' consumption (Table 2).

Table 2. Diet composition of cetaceans in the study area. All values are percentages. Empty cells indicate that a prey item was never found whereas "0.0" indicates that it was found in very small amounts.

Prey	Minke whale	Fin whale	Humpback whale	Long-finned pilot whale	Harbour porpoise	White-beaked dolphin	White-sided dolphin	Mean diet
Large cod	0.0				0.3	6.8		0.4
Small cod	5.0				0.3	20.4		2.2
American plaice						0.1		0.0
Redfish					5.9			0.3
Large demersals					0.0	13.8		0.8
Small demersals					0.1	0.8	45.4	5.0
Capelin	75.0	75.0	75.0		40.2			52.4
Sand lance		8.3	8.3					4.1
Large pelagics					0.0		5.6	0.6
Pisci. small pelagics	5.0		8.3	100.0	4.3	58.1	45.7	21.0
Plank. small pelagics	10.0	8.3			48.9			7.8
Shrimp					0.0		3.3	0.4
Large zooplankton	5.0	8.3	8.3		0.0			5.0

Due to the uncertainties with diet data, we also used the diet composition found by Bundy et al. (2000) in the Newfoundland–Labrador Shelf (1985–1987 period) to construct the diet composition of cetaceans used in modelling (Table 3).

Table 3. Diet composition of cetaceans used in modelling. Est: diet estimates by the inverse model; TRN: number of trophic relations; SD: standard deviation. All values are percentages except TRN. Empty cells indicate that a prey item was never found whereas "0.0" indicates that it was found in very small amounts.

	Cetaceans				
Prey	Mean	±SD	Min	Max	Est
Large cod	0.2	0.3	0.0	0.4	0.2
Small cod	1.7	0.7	1.2	2.2	1.9
Large Green. halibut					
Small Green. halibut					
American plaice	0.0	0.0	0.0	0.0	0.0
Flounders					
Skates					
Redfish	0.2	0.2	0.0	0.3	0.2
Large demersals	2.1	1.7	0.8	3.3	3.0
Small demersals	1.7	2.3	0.1	3.3	1.9
Capelin	50.7	2.5	48.9	52.4	49.8
Sand lance	4.6	0.8	4.1	5.2	4.8
Arctic cod					
Large pelagics	0.3	0.4	0.0	0.5	0.3
Pisci. small pelagics	18.7	3.4	16.3	21.1	18.9
Plank. small pelagics	7.9	6.9	3.0	12.8	5.2
Shrimp	0.1	0.1	0.0	0.2	0.1
Large crustacea					
Echinoderms					
Molluscs					
Polychaetes					
Other bent. inver.					
Large zooplankton	7.8	3.7	5.1	10.4	6.5
Small zooplankton	4.2	5.9	0.0	8.3	7.2
Phytoplankton					
Detritus					
Total	100.0		79.5	120.4	100.0
TRN	14				

Seals

Background

Four species of pinnipeds occur in the Gulf of St. Lawrence. The harp seal (*Phoca groenlandica*) is the most abundant pinniped in Atlantic Canada and usually summers in the

Canadian Arctic or northwest Greenland before returning south to winter in Canadian Atlantic waters. Reproduction occurs in March on the pack ice in the Gulf of St. Lawrence (Gulf herd) and off southern Labrador (Front herd). In the Gulf, animals whelp in two areas: off the lower North Shore and near the Îles-de-la-Madeleine (Sergeant 1991). During the 1985–1987 period, the northwest Atlantic population was estimated to be 3,489,441 (Healey and Stenson 2000), with an average of 2.5% of the pups and juveniles and 4.1% of the adults found in the Gulf of St Lawrence (Hammill and Stenson 2000).

Hooded seals (*Cystophora cristata*), which are larger than harp seals, are the least abundant pinniped within the study area, with an average population of 8,698 individuals for 1985–87 (M. Hammill, DFO, Institut Maurice-Lamontagne, Mont-Joli, Québec, unpublished data). Only 36.2% of these animals are situated in zones 4RS (Hammill and Stenson 2000). In the northwest Atlantic, most pups are born in March on pack ice off northeast Newfoundland, with smaller whelping concentrations located in Davis Strait and the Gulf of St. Lawrence. After leaving the whelping patch in late March, adults from the Gulf of St. Lawrence move to the northern Gulf where they remain until mid-May, when they return to Greenland. Hooded seals have been protected in the Gulf since 1972 (Hammill et al. 1997).

The major grey seal (*Halichoerus grypus*) breeding colonies in eastern Canada are located on Sable Island and in the southern Gulf of St. Lawrence (Mansfield and Beck 1977). After breeding, both juveniles and adults disperse widely over eastern Canada. Large numbers are known to feed in the northern Gulf of St. Lawrence, which makes it the second most abundant pinniped of the zone (Hammill and Stenson 2000). According to mark–recapture experiments from 1984 to 1990, the population in 1985–87 averaged 39,320 individuals from the Gulf herd and 33,486 individuals from the Sable Island herd (M. Hammill, unpublished data), with 33.7% of the Gulf herd and 7.9% of the Sable Island herd found in zones 4RS (Hammill and Stenson 2000).

Harbour seals (*Phoca vitulina*) are found throughout eastern Canada (Boulva and McLaren 1979), occurring in small groups dispersed along coastal areas (Lesage et al. 1995). Harbour seal abundance in Atlantic Canada has never been evaluated by direct survey. Based on questionnaires sent to fisheries officers, Boulva and McLaren (1979) estimated that there were about 13,000 animals in eastern Canada. Hammill and Stenson (2000) modelled population changes for this species and estimated that the average population was 18,305 for 1985–87 (M. Hammill, unpublished data), with 26.4% of animals situated in the northern Gulf (Hammill and Stenson 2000).

Catch

Commercial catches (total numbers) for harp, grey, and hooded seals are reported in the Atlantic resource management landing reports from 1986 to 1997 (DFO, Headquarters/National Capital Region, Ottawa, Ontario, unpublished data; Stenson et al. 2000). Catches were divided into pups (young of the year) and animals one year and older (Sjare et al. 1996). Numbers-at-age were multiplied by mean mass-at-age (Hammill and Stenson 2000) to obtain total catches in tons. For harp seals, the mean annual catch for 1985–1987 was estimated at $5.82 \times 10^{-3} \pm 1.63 \times 10^{-3}$ t km^{-2}. The inverse solution estimated a catch of 4.49×10^{-3} t km^{-2} yr^{-1}.

The number of hooded seals removed from the northern Gulf of St. Lawrence (data from the west coast of Newfoundland, the Gulf, and Québec's North Shore) was obtained directly from catch statistics. An average of 108 seals were caught each year, but numbers varied greatly among years, from 0 to 216. These values resulted in an estimated mean annual catch of $1.85 \times 10^{-4} \pm 2.60 \times 10^{-4}$ t km^{-2}. The inverse solution estimated a catch of 1.33×10^{-4} t km^{-2} yr^{-1}.

The grey seal is not hunted commercially in Canadian waters. However, this species is subject to a scientific removal and bounty hunting. Harvesting activity has declined over the last 50 years and the bounty was eliminated in 1992 (Hammill et al. 1998). These removals resulted in an estimated mean annual catch of $6.41 \times 10^{-4} \pm 4.02 \times 10^{-4}$ t km^{-2}. The inverse solution estimated a catch of 5.62×10^{-4} t km^{-2} yr^{-1}.

Even though harbour seals have been protected since 1976 (Boulva and McLaren 1979), some losses may have occurred through by-catch by commercial fisheries. However, there is no data available to assess this loss, so catch was not entered in the model.

Biomass

Biomass was estimated by multiplying abundance by mean mass-at-age (Hammill and Stenson 2000). The number of seals in each age class was obtained from an updated version of the population model of Hammill and Stenson (2000), extrapolated backwards to 1985. Biomass was adjusted for residence time in 4RS (Hammill and Stenson 2000), resulting in mean annual biomass estimates for the 1985–1987 period of 0.085 ± 0.005 t km^{-2} for harp seals, 0.003 ± 0.000 t km^{-2} for hooded seals, 0.018 ± 0.001 t km^{-2} for grey seals, and 0.003 ± 0.000 t km^{-2} for harbour seals.

Production

The P/B ratio was estimated by dividing the pup biomass by the uncorrected population biomass (minimum value) for the northern Gulf of St. Lawrence as reported in an updated version of the population model of Hammill and Stenson (2000) for the 1985–1987 period. The P/B ratios were 0.071 ± 0.004 yr^{-1} for harp seals, 0.061 ± 0.000 yr^{-1} for hooded seals, 0.079 ± 0.000 yr^{-1} for grey seals, and 0.071 ± 0.000 yr^{-1} for harbour seals. This resulted in production values of 0.010 t km^{-2} yr^{-1} for harp seals, 0.0002 t km^{-2} yr^{-1} for hooded seals, 0.0015 t km^{-2} yr^{-1} for grey seals, and 0.0002 t km^{-2} yr^{-1} for harbour seals. Based on the annual consumption values of Hammill and Stenson (2000) (see below) and the upper GE limit (1%; values based on the lower GE limit of 0.1% were not realistic), we obtained other production values: 0.004 t km^{-2} yr^{-1} for harp seals, 0.0004 t km^{-2} yr^{-1} for hooded seals, 0.0005 t km^{-2} yr^{-1} for grey seals, and 0.0001 t km^{-2} yr^{-1} for harbour seals. Thus, we obtained mean annual production values of 0.007 ± 0.04 t km^{-2} yr^{-1} for harp seals, 0.003 ± 0.001 t km^{-2} yr^{-1} for hooded seals, 0.0010 ± 0.0007 t km^{-2} yr^{-1} for grey seals, and 0.0001 ± 0.0001 t km^{-2} yr^{-1} for harbour seals. The inverse solution estimated production values of 0.006 t km^{-2} yr^{-1} (P/B = 0.070 yr^{-1}) for harp seals, 0.0003 t km^{-2} yr^{-1} (P/B = 0.089 yr^{-1}) for hooded seals, 0.0010 t km^{-2} yr^{-1} (P/B = 0.053 yr^{-1}) for grey seals, and 0.0001 t km^{-2} yr^{-1} (P/B = 0.053 yr^{-1}) for harbour seals.

Consumption

Total annual consumption of prey by each seal species in the study area was estimated from an updated version of the consumption model of Hammill and Stenson (2000). The mean annual consumption values were 0.371 ± 0.021 t km^{-2} yr^{-1} for harp seals, 0.042 ± 0.002 t km^{-2} yr^{-1} for hooded seals, 0.052 ± 0.006 t km^{-2} yr^{-1} for grey seals, and 0.010 ± 0.001 t km^{-2} yr^{-1} for harbour seals. The annual consumption ranges were 0.350–0.392 t km^{-2} yr^{-1} for harp seals, 0.040–0.044 t km^{-2} yr^{-1} for hooded seals, 0.026–0.081 t km^{-2} yr^{-1} for grey seals, and 0.010–0.011 t km^{-2} yr^{-1} for harbour seals. Based on the previous mean annual production and the upper GE limit (1%; values based on the lower GE limit of 0.1% were not realistic), we obtained other consumption values: 0.672 t km^{-2} yr^{-1} for harp seals, 0.032 t km^{-2} yr^{-1} for hooded seals, 0.103 t km^{-2} yr^{-1} for grey seals, and 0.015 t km^{-2} yr^{-1} for harbour seals. Finally, based on these different values, we estimated the lower and upper consumption limits used as constraints in inverse modelling (see Table 19). The resulting mean consumption values were 0.511 ± 0.228 t km^{-2} yr^{-1} for harp seals, 0.038 ± 0.009 t km^{-2} yr^{-1} for hooded seals, 0.064 ± 0.054 t km^{-2} yr^{-1} for grey seals, and 0.012 ± 0.004 t km^{-2} yr^{-1} for harbour seals. The inverse solution estimated consumption values of 0.609 t km^{-2} yr^{-1} ($Q/B = 7.193$ yr^{-1}) for harp seals, 0.034 t km^{-2} yr^{-1} ($Q/B = 9.901$ yr^{-1}) for hooded seals, 0.100 t km^{-2} yr^{-1} ($Q/B = 5.588$ yr^{-1}) for grey seals, and 0.014 t km^{-2} yr^{-1} ($Q/B = 5.705$ yr^{-1}) for harbour seals.

Diet composition

For harp seals, diet information was available for nearshore waters of the northwest Atlantic during 1990–1993 (Lawson et al. 1995), for inshore 2J3KL during 1991–1992 (Lawson et al. 1993), and for the St. Lawrence Estuary (Murie and Lavigne 1991; Beck et al. 1993; Lawson et al. 1995; Hammill and Stenson 2000). According to these diet studies, the main prey species were, in order of importance, capelin, Atlantic herring, Atlantic cod, redfish, and Arctic cod (*Boreogadus saida*).

There was no diet information available for hooded seals in the northern Gulf. Hammill et al. (1997) used a diet based on work done by Ross (1993), where the main prey items were young Greenland halibut, flounders, and small pelagic feeders. Other information about this species was based on offshore samples from NAFO zones 2J3KL collected from 1991–1993 (Lawson et al. 1993). In that study, stomachs examined contained mainly Atlantic cod, witch flounder, and squid. Hammill and Stenson (2000) used a diet made up of samples from Ross (1993) and Lawson and Stenson (DFO, Northwest Atlantic Fisheries Centre, St. John's, Newfoundland, unpublished data) in which major prey for the Gulf and 2J3KL inshore regions were Greenland halibut, redfish, Arctic cod, and herring.

Several studies have examined the diet composition of grey seals in the northern Gulf of St. Lawrence. These have determined that Atlantic cod, herring, lumpfish (*Cyclopterus lumpus*), wolffish, capelin, mackerel, and ocean pout were the main prey items of this species (Benoit and Bowen 1990; Murie and Lavigne 1992; Proust 1996; Hammill and Stenson 2000).

Harbour seal diet composition was examined in two inshore habitats of Atlantic Canada (lower Bay of Fundy and the north-eastern coast of Nova Scotia) between 1988 and 1992 (Bowen and Harrison 1996). For the 250 food-containing stomachs examined, the major prey were Atlantic herring, squid, pollock (*Pollachius virens*), and Atlantic cod.

The upper and lower limits resulting from these different diet studies, as well as the output diets estimated by the inverse model for the northern Gulf of St. Lawrence (mid-1980s), are shown in Table 4.

Table 4. Diet compositions of seals used in modelling. Est: diet estimates by the inverse model; TRN: number of trophic relations; SD: standard deviation. All values are percentages except TRN. Groups with indicated CV (available only as point estimates): Min = mean - (mean x 50%), Max = mean + (mean x 50%). Empty cells indicate that a prey item was never found whereas "0.0" indicates that it was found in very small amounts.

	Harp seals					Hooded seals				
Prey	Mean	± SD	Min	Max	Est	Mean	± SD	Min	Max	Est
Large cod	1.2	2.8	0.0	3.9	2.8	10.5	14.7	0.5	21.4	14.8
Small cod	3.3	7.5	0.0	10.7	8.1	10.2	14.3	0.5	20.8	14.4
Large Green. halibut	2.1	4.7	0.0	6.6	4.0	1.7	2.5	0.0	3.6	2.1
Small Green. halibut	2.3	5.2	0.0	7.4	5.1	24.0	33.7	1.3	48.9	25.3
American plaice	4.1	9.4	0.0	13.2	5.6					
Flounders	6.9	15.7	0.0	22.2	4.1	14.6	21.6	0.0	30.6	11.3
Skates	0.0	0.0	0.0	0.0	0.0					
Redfish	4.6	10.5	0.0	14.9	6.0	13.1	12.4	4.9	22.5	11.8
Large demersals	3.3	7.6	0.0	10.8	9.8	1.2	1.7	0.0	2.4	1.7
Small demersals	2.2	4.0	0.8	6.4	2.0	5.7	8.5	0.0	12.0	6.0
Capelin	29.2	60.1	4.6	89.6	30.6	0.5	0.4	0.3	0.8	0.5
Sand lance	2.9	6.7	0.0	9.5	5.8					
Arctic cod	16.9	38.7	0.0	54.7	0.0	8.0	9.8	1.4	15.3	2.8
Large pelagics	0.2	0.3	0.0	0.5	0.2					
Pisci. small pelagics	2.2	5.0	0.0	7.0	2.7	3.4	5.1	0.0	7.2	4.3
Plank. small pelagics	6.2	14.1	0.0	20.0	4.3	7.0	10.4	0.0	14.7	5.0
Shrimp	2.1	4.8	0.0	6.8	0.2					
Large crustacea	0.9	2.0	0.0	2.8	0.5					
Echinoderms										
Molluscs										
Polychaetes										
Other bent. inver.	1.8	4.2	0.0	5.9	3.6					
Large zooplankton	7.6	17.4	0.0	24.7	4.7					
Small zooplankton										
Phytoplankton										
Detritus										
Total	100.0		5.5	317.6	100.0	100.0		8.9	200.2	100.0
TRN	20					12				

Table 4. Cont.

Prey	Grey seals					Harbour seals (CV= 50%)				
	Mean	± SD	Min	Max	Est	Mean	± SD	Min	Max	Est
Large cod	11.0	15.4	2.0	23.7	13.3	1.9		0.9	2.8	2.0
Small cod	10.7	15.0	1.9	23.1	13.4	5.6		2.8	8.4	5.9
Large Green. halibut	0.0	0.0	0.0	0.0	0.0					
Small Green. halibut	0.3	0.5	0.0	0.7	0.3					
American plaice	5.3	8.7	0.0	12.4	7.8					
Flounders	8.4	13.8	0.0	19.6	7.0	1.8		0.9	2.7	1.9
Skates	17.3	28.7	0.0	40.5	6.1	0.1		0.1	0.2	0.1
Redfish	0.0	0.1	0.0	0.1	0.0	0.4		0.2	0.6	0.4
Large demersals	11.0	4.7	9.5	16.2	13.4	2.7		1.3	4.0	3.1
Small demersals	12.8	19.2	1.4	28.5	11.0	3.0		1.5	4.4	2.9
Capelin	8.3	12.9	0.6	18.8	9.6	5.9		2.9	8.8	6.7
Sand lance	5.7	9.5	0.0	13.4	10.0					
Arctic cod										
Large pelagics	0.6	1.0	0.0	1.4	1.3	8.7		4.4	13.1	9.9
Pisci. small pelagics	2.7	4.4	0.0	6.3	3.3	29.9		14.9	44.8	34.1
Plank. small pelagics	5.8	9.6	0.1	13.6	3.5	33.5		16.8	50.3	26.3
Shrimp	0.0	0.0	0.0	0.0	0.0	5.9		3.0	8.9	6.0
Large crustacea	0.1	0.1	0.0	0.2	0.1	0.4		0.2	0.6	0.4
Echinoderms										
Molluscs						0.2		0.1	0.3	0.2
Polychaetes										
Other bent. inver.	0.0	0.0	0.0	0.0	0.0	0.1		0.1	0.2	0.1
Large zooplankton	0.0	0.0	0.0	0.0	0.0					
Small zooplankton										
Phytoplankton										
Detritus										
Total	100.0		15.5	218.5	100.0	100.0		50.0	150.0	100.0
TRN	19					12				

Seabirds

Background

In the northern Gulf of St. Lawrence, 64.5% of seabirds are found inshore while 35.5% are distributed offshore (Cairns et al. 1991). Inshore seabirds breed in a large number of smaller colonies dispersed along the coastline while offshore species breed in a small number of large colonies (Lack 1967). Major inshore species breeding in the region are the great cormorant (*Phalacrocorax carbo*), double-crested cormorant (*Phalacrocorax auritus*), ring-billed gull

(*Larus delawarensis*), herring gull (*Larus argentatus*), great black-backed gull (*Larus marinus*), common tern (*Sterna hirundo*), Arctic tern (*Sterna paradisaea*), and black guillemot (*Cepphus grylle*). Major offshore species that breed in the region are the northern gannet (*Morus bassanus*), black-legged kittiwake (*Rissa tridactyla*), common murre (*Uria aalge*), razorbill (*Alca torda*), Atlantic puffin (*Fratercula arctica*), and Leach's storm-petrel (*Oceanodroma leucorhoa*). These species occur at different times of the year within the study area (Table 5).

Catch/Anthropogenic mortality

There are three primary sources of anthropogenic mortality for seabirds in the region: 1) by-catch in fishing gear, 2) hunting, and 3) oil pollution (Montevecchi and Tuck 1987). In the northern Gulf, a few species of seabirds such as ducks and guillemots are hunted for food along Québec's North Shore. Considerable numbers of seabirds (mostly alcids, i.e., murres and puffins, but also others, e.g., gannets) are also caught as by-catch in fishing gear. Bundy et al. (2000) assumed that mortality coming from hunting, by-catch, and maritime traffic amounts to 0.001 t km^{-2} per year. On the basis of information for seabirds from Newfoundland (NAFO zones 2J3KL) (Bundy et al. 2000), we estimated a catch rate (0.001 t km^{-2} yr^{-1} divided by the seabird biomass, 0.012 t km^{-2}) for the Newfoundland ecosystem and we applied it to the 4RS zone. It totalled 3.35×10^{-4} t km^{-2} yr^{-1} of seabirds being removed annually from the study area through anthropogenic mortality. The inverse solution estimated a catch of 3.40×10^{-4} t km^{-2} yr^{-1}.

Biomass

Unlike the open Atlantic coast of Canada, the Gulf of St. Lawrence is not frequented by large numbers of trans-oceanic and trans-equatorial migrants (Brown 1986). Thus, population estimates based on counts of breeding colonies can be used (Cairns et al. 1990). Data on body mass and population estimates for various seabirds were derived from Chapdelaine (unpublished data). In order to estimate biomass density, we assumed that seabirds were distributed uniformly throughout NAFO zones 4RST. Consequently, biomass was determined by taking the number of birds, multiplied by their respective biomass, and divided by the whole 4RST bird inventory area (214,000 km^2) instead of the value usually used for the other groups (the sampling area for zones 4RS). For species that breed within NAFO zones 4RST, population estimates (Table 5) were calculated as follows (Chapdelaine, unpublished data):

Population estimate = breeding pairs x 2
+ [0.60 x breeding pairs x 2] nestlings
+ [0.80 x breeding pairs (offshore species)] (5)

or

Population estimate = breeding pairs x 2
+ [0.60 x breeding pairs x 2] nestlings
+[1.0 x breeding pairs (inshore species)] (6)

The total biomass estimate for the 4RS study area is 859 t or 0.004 t km^{-2} (Table 5).

Table 5. Approximate period of occupation, population size, and average body mass and biomass for the main species of seabirds that breed within the study area (NAFO zones 4RS), or breed primarily or completely outside but occur in the study area or are nestlings. Note that the shaded section indicates inshore seabirds while the unshaded section corresponds to offshore seabirds.

Species	Period of occupation	Population (numbers) of breeders	Population (numbers) of non-breeders and nestlings	Individual mass (kg)	Adjusted average biomass (t)
Great cormorant	Apr-Oct	4,968	3,478	2.25	11.085
Double-crested cormorant	Apr-Oct	78,000	54,600	1.67	205.148
Ring-billed gull	Apr-Oct	66,784	53,427	0.50	35.060
Herring gull	Mar-Dec	95,774	76,619	1.12	160.861
Black-headed gull	Apr-Oct	20	16	0.28	0.006
Great black-backed gull	Mar-Dec	19,472	15,578	1.68	49.068
Common tern	May-Sep	52,536	42,029	0.12	4.729
Caspian tern	May-Sep	22	18	0.61	0.010
Arctic tern	May-Sep	2,010	1,608	0.11	0.166
Black guillemot	Jan-Dec	9,524	6,667	0.40	6.477
Leach's storm-petrel	May-Oct	1,036	725	0.05	0.044
Northern gannet	Apr-Oct	84,248	58,974	3.20	267.333
Black-legged kittiwake	Apr-Oct	16,8752	118,126	0.44	73.628
Common murre	May-Sep	89,320	62,524	0.99	87.685
Thick-billed murre	Apr-Oct	24	17	0.93	0.022
Razorbill	Apr-Oct	16,500	11,550	0.72	11.781
Atlantic puffin	Apr-Oct	48,348	33,844	0.46	22.054
TOTAL	**Jan-Dec**	**651,141**	**539,790**	-	**859.176**

Production

An energetic model developed for Gulf of St. Lawrence seabirds (Chapdelaine, unpublished data) indicates that there are a total of 221,201 nestlings produced each year for all species combined (calculated by assuming that nestlings = number of breeding pairs x 0.6). Multiplying the number of nestlings by the average mass of each species results in a total annual production of 0.001 t km^{-2} yr^{-1} and a P/B ratio of 0.276 yr^{-1}. The inverse solution estimated a production of 0.001 t km^{-2} yr^{-1}, representing a P/B of 0.289 yr^{-1}.

Consumption

Estimated food consumption for seabirds in the northern Gulf is 108,419 t yr^{-1} (Chapdelaine, unpublished data). Assuming that consumption is evenly distributed throughout the region results in an estimated Q/B ratio of 126.179 yr^{-1} and an annual consumption of 0.507 t km^{-2} yr^{-1}. Based on the previous annual production and the upper GE limit (1%; the value based on the lower GE limit of 0.1% was not realistic), we obtained another consumption estimate of

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0.111 t km^{-2} yr^{-1}. This resulted in a mean consumption of 0.309 ± 0.280 t km^{-2} yr^{-1}. The inverse solution estimated a consumption of 0.163 t km^{-2} yr^{-1}, representing a Q/B of 40.618 yr^{-1}.

Diet composition

Seabirds within the study area feed at a variety of trophic levels with most prey being small pelagic fish, benthic invertebrates, and pelagic crustaceans (Cairns et al. 1990). Great cormorants feed mostly on benthic fish, primarily flatfish and cunners (*Tautogolabrus adspersus*), while double-crested cormorants prey heavily on flatfish, sculpins (*Myoxocephalus* sp.), rock gunnels (*Pholis gunnellus*), and sand lance (*Ammodytes americanus*). The only data available from the Gulf of St. Lawrence for black guillemot showed that chicks are fed primarily with benthic fish, particularly sculpins, blennies, and tomcod (*Microgadus tomcod*) (Cairns 1981). Northern gannet, the largest breeding seabird species in the study area, preys on large pelagic species such as mackerel and Atlantic saury (*Scomberesox saurus*), but also on sand lance (Burton 1980). Herring gulls, which are the most abundant species in the study area, feed primarily on small pelagic fish and non-marine food (Threlfall 1968; Haycock and Threlfall 1975; Pierroti 1983), but quantitative dietary data from the Gulf are generally lacking for this species as well as for all other gulls, terns, storm-petrels, kittiwakes, and offshore alcids (Cairns et al. 1990). The diets of Arctic tern, recorded on Québec's North Shore (NAFO zone 4S; Chapdelaine et al. 1985), as well as the diet of the common tern, the most abundant species in the eastern part of the area (NAFO zone 4R), consisted mainly of capelin, sand lance, and pelagic invertebrates. Black-legged kittiwakes are the most abundant species in the western part of the study area (NAFO zone 4S) and feed primarily on copepods and euphausiids (Threlfall 1968; Maunder and Threlfall 1972). The final seabird diet was modified following Cairns et al. (1990) and Chapdelaine (unpublished data), who used all available information for the Gulf of St. Lawrence as well as extrapolated information from the closest ecosystems to create a complete diet for all seabird species found in the Gulf of St. Lawrence (north and south, NAFO zones 4RST). There is no diet data available for Leach's storm-petrel, kittiwakes, murres, razorbills, or Atlantic puffins from the northern Gulf. Information for these species has been extrapolated from Labrador, eastern Newfoundland, and Nova Scotia (Bundy et al. 2000). Based on these different studies, we estimated the resulting diet composition of seabirds used in modelling for the northern Gulf of St. Lawrence (mid-1980s) (Table 6).

Table 6. Diet composition of seabirds used in modelling. Est: diet estimates by the inverse model; TRN: number of trophic relations; SD: standard deviation. All values are percentages except TRN. Empty cells indicate that a prey item was never found whereas "0.0" indicates that it was found in very small amounts.

	Seabirds				
Prey	Mean	±SD	Min	Max	Est
Large cod					
Small cod	0.2	0.4	0.0	0.5	0.2
Large Green. halibut					
Small Green. halibut	0.4	0.6	0.0	0.8	0.4
American plaice	0.4	0.6	0.0	0.8	0.4
Flounders	0.4	0.6	0.0	0.8	0.4
Skates	0.4	0.6	0.0	0.8	0.4
Redfish					
Large demersals					
Small demersals	8.3	10.8	1.6	16.9	3.5
Capelin	41.0	34.0	21.9	70.0	31.9
Sand lance	27.9	37.2	5.0	57.6	48.0
Arctic cod	2.7	4.2	0.0	6.0	0.0
Large pelagics	0.0	0.1	0.0	0.1	0.0
Pisci. small pelagics	9.7	15.1	0.2	21.5	8.4
Plank. small pelagics	2.2	2.3	0.8	4.0	1.8
Shrimp	0.6	1.0	0.0	1.4	0.1
Large crustacea					
Echinoderms					
Molluscs	0.0	0.1	0.0	0.1	0.0
Polychaetes					
Other bent. inver.	0.6	1.0	0.0	1.4	0.7
Large zooplankton	5.0	7.8	0.0	11.1	3.7
Small zooplankton	0.2	0.4	0.0	0.5	0.2
Phytoplankton					
Detritus					
Total	100.0		29.6	194.5	100.0
TRN	17				

Atlantic cod

Background

The northern Gulf cod stock overwinters in the deep waters off south-western Newfoundland and then returns to the Gulf, moving northwards off Newfoundland's west coast

(NAFO zone 4R). Spawning takes place mainly during April and May in Esquiman Channel. During summer, the population migrates to the warmer coastal waters of Québec's lower North Shore and the west coast of Newfoundland.

Commercial catches increased considerably during the late 1950s and 1960s, with the stock declining to low levels by the mid to late 1970s. Following this decline, there was a period of recovery during the early 1980s before the stock collapsed in the early 1990s (Fréchet and Schwab 1998).

For the purpose of this study, Atlantic cod were divided into adults and juveniles, or more precisely, into large and small fish. Biomass and catch data were collected from NAFO zones 3Pn4RS. Northern Gulf cod of age 4+ generally represent fish ≥ 35 cm of length, at which size cod become more piscivorous and begin to be recruited to the commercial fishery (Lesage et al. 2001; Fréchet et al. 2003).

Catch

Catch data for cod age 4+ in NAFO zones 3Pn4RS were available for the 1985–87 period (Fréchet and Gagnon 1993). Since cod from these three zones are considered to be part of the same stock, catches from 3Pn were included in the model (M. Castonguay, DFO, Institut Maurice-Lamontagne, Mont-Joli, Québec, personal communication). In the absence of information for this species, it was assumed that there were no discards or by-catch. Mean catch of 4+ cod for 1985–1987 was $7.63 \times 10^{-1} \pm 1.09 \times 10^{-1}$ t km^{-2} yr^{-1}. For the small cod group, the accidental catches were estimated at $8.18 \times 10^{-4} \pm 6.65\ 10^{-4}$ t km^{-2} yr^{-1} (Fréchet and Gagnon 1993). The inverse solution estimated catch values of 7.55×10^{-1} and 8.55×10^{-4} t km^{-2} yr^{-1} for large and small cod, respectively.

Biomass

The biomass of 4+ cod was based on virtual population analysis estimates of cod biomass at the beginning of the year. The estimated average biomass of 4+ cod was 407,868 t or 3.929 t km^{-2} (SD = 0.813 t km^{-2}).

Assuming an annual instantaneous rate of natural mortality of 0.6 (since young fish are likely to have a higher natural mortality rate than older fish; M. Castonguay, personal communication) and a negligible catch of small cod, the numbers of 0-, 1-, and 2-year-old fish were estimated by back-calculation using an equation derived from Ricker (1980):

$$N_{i-1} = N_i / e^{-z} \qquad (7)$$

where N is abundance, i is year class, and Z is total mortality (here equal to natural mortality). Mean body mass was then multiplied by the abundance of each age class in order to obtain the biomass for the given group (this was not done for age 3 cod, for which biomass was directly taken from the VPA). Values of mean body mass were 0.010, 0.035, and 0.134 kg for fish of 0, 1, and 2 years of age, respectively (DFO, groundfish survey database, unpublished data). The biomass of age groups 0 to 3 were then summed in order to obtain a biomass estimate of small cod for each of the three years considered. This method yielded a mean annual biomass for small cod of 170,545 t or 1.643 t km^{-2} (SD = 0.470 t km^{-2}).

Production

P/B of large cod was estimated by catch-curve analysis of groundfish survey data from NAFO zones 4RS for the 1985–1987 period. The estimate of total mortality ($Z = 0.755$ yr^{-1}) was determined from the slope of the regression line fitted to the downward side of the catch curve. Since we assume a steady state (no year-to-year change in biomass), total mortality is equal to the P/B ratio (0.755 yr^{-1} or 3.075 t km^{-2} yr^{-1}) of cod in 1985–1987 (Allen 1971). Another method was also used to estimate production, which was equivalent to biomass multiplied by natural mortality (M) plus catch. Natural mortality for large cod was estimated at 0.20 yr^{-1} (Fréchet and Gagnon 1993). We obtained an annual production of 1.549 t km^{-2} yr^{-1}. This resulted in a mean annual production of 2.312 ± 1.079 t km^{-2} yr^{-1}. The inverse solution estimated a production of 1.649 t km^{-2} yr^{-1}, representing a P/B of 0.420 yr^{-1}.

The P/B ratio for juvenile cod (0–3 years) is the total mortality assumed for the back-calculation of numbers at age described above (0.600 yr^{-1}). Multiplying this value by the minimum and maximum biomass values for small cod, we estimated a production range between 0.669 and 1.210 t km^{-2} yr^{-1}, corresponding to an annual production of 0.986 ± 0.383 t km^{-2} yr^{-1}. The inverse solution estimated a production of 0.747 t km^{-2} yr^{-1}, representing a P/B of 0.455 yr^{-1}.

Consumption

A range of Q/B values was used to estimate the mean Q/B ratio for large cod (Table 7). These values were based on different studies of food consumption by cod populations of other regions (Palomares and Pauly 1989; Pauly 1989) as well as in the Gulf of St. Lawrence (Waiwood et al. 1980). The Q/B ratios for large cod varied between 1.41 and 4.55 yr^{-1}, corresponding to a consumption range between 5.540 and 17.877 t km^{-2} yr^{-1}. Based on the previous mean production (2.312 t km^{-2} yr^{-1}) for large cod and the minimum and maximum GE limits (10–30%), we obtained consumption values of 7.707 and 23.120 t km^{-2} yr^{-1}. The resulting lower and upper consumption limits were thus 5.540 and 23.120 t km^{-2} yr^{-1}, corresponding to a mean consumption of 14.330 ± 8.339 t km^{-2} yr^{-1}. The inverse solution estimated a consumption of 7.580 t km^{-2} yr^{-1}, representing a Q/B of 1.929 yr^{-1}.

Four studies were used to estimate the mean Q/B ratio for small cod (Daan 1973; Waiwood et al. 1980; Hawkins et al. 1985; Grundwald and Koster 1994). Q/B estimates were extrapolated from food intake measurements (daily or yearly consumption) and body mass or biomass of fish under study. This approach yielded Q/B ratios of 3.250 yr^{-1} (Waiwood et al. 1980), 7.271 yr^{-1} (Daan 1973), 10.730 yr^{-1} (Hawkins et al. 1985), and 2.564 yr^{-1} (Grundwald and Koster 1994). The Q/B ratios for small cod varied between 2.564 and 10.730 yr^{-1}, corresponding to a consumption range between 4.212 and 17.628 t km^{-2} yr^{-1}. Based on the previous mean production (0.986 t km^{-2} yr^{-1}) for small cod and the minimum and maximum GE limits (10–30%), we obtained consumption values of 3.286 and 9.857 t km^{-2} yr^{-1}. The resulting lower and upper consumption limits were thus 3.286 and 17.628 t km^{-2} yr^{-1}, corresponding to a mean consumption of 10.457 ±

6.595 t km^{-2} yr^{-1}. The inverse solution estimated a consumption of 3.712 t km^{-2} yr^{-1}, representing a Q/B of 2.260 yr^{-1}.

Table 7. Q/B ratios for Atlantic cod in different regions of the world. Data are from Waiwood et al. (1980)[1], Palomares and Pauly (1989)[2], Pauly (1989)[3], and Froese and Pauly (2002)[4].

Q/B	Region
1.41	North of Norway[3, 4]
1.94	Kattegat, Denmark[3, 4]
2.17	East Baltic Sea[3, 4]
2.19	Georges Bank[3, 4]
2.26	North Sea[2, 3, 4]
2.34	Barents Sea[3, 4]
2.58	West Baltic Sea[2, 3, 4]
3.41	Irish Sea[3, 4]
3.43	Northwest Atlantic[3, 4]
4.08	Iceland[3, 4]
4.36	Faeroe Islands[3, 4]
4.55	Scotland[3, 4]
2.7	West Baltic Sea[2]
2.29	North Sea[2]
1.96	Southwestern Gulf of St. Lawrence[1]

Diet composition

Stomach content data were available from NAFO zones 4RS for spring (April-June), summer (July-November), and winter (December-March) of 1983–1988 (D. Chabot, DFO, Institut Maurice-Lamontagne, Mont-Joli, Québec, unpublished data). Sampling was length-stratified and covered the inshore and offshore zones for all seasons. In winter, inshore sampling was reduced due to ice cover over most of the northern Gulf of St. Lawrence. Information on empty stomachs is unavailable for this database. Sample sizes for spring, summer, and winter were 401, 310, and 1463, respectively, for large cod and 50, 35, and 212 for small cod. Although cod forage most intensively during the summer (fullness index, excluding empty stomachs, was 1.93, 2.38, and 1.51 for spring, summer, and winter in large cod and 1.56, 3.03, and 1.72 in small cod), most samples (67% in large cod, 71% in small cod) were collected during winter. Therefore, to estimate a diet most representative of the entire year, average diets were calculated for each season (in % mass) and then averaged into a final diet using the product "fullness index x season duration (in months)" as a weighting factor. Cod stomach content data were also available for the same region in the summer and winter of 1978–79 (D. Chabot, unpublished data). This second sample was analyzed in the same manner, except that empty stomachs were included in the analysis, as this results in a better estimate of seasonal fluctuations in stomach fullness. Sample sizes for summer and winter, respectively, were 323 and 634 for large cod and 56 and 154 for small cod. Seasonal values of stomach fullness in large cod were 0.87 and 0.31 in summer and winter, respectively. For small cod, stomach fullness was 0.59 and 0.55 in summer and winter, respectively. These two diets were used as constraints in inverse modelling. For large cod, we used also the study of Minet and Perodou (1978) taking the data from the Gulf of St. Lawrence. Overall, the most important prey items of large cod, in percent mass of stomach content, were capelin, redfish, small planktonic pelagic fish, and large zooplankton, which together accounted for 66.1% of the diet (Table 8). The most important prey items of small cod were large zooplankton, capelin, and shrimp (90.6%) (Table 8).

Table 8. Diet composition of large and small cod used in modelling. Est: diet estimates by the inverse model; TRN: number of trophic relations; SD: standard deviation. All values are percentages except TRN. Empty cells indicate that a prey item was never found whereas "0.0" indicates that it was found in very small amounts.

	Large cod (> 35 cm)					Small cod (≤ 35 cm)				
Prey	Mean	± SD	Min	Max	Est	Mean	± SD	Min	Max	Est
Large cod										
Small cod	2.7	2.7	0.8	5.8	4.8	0.2	0.2	0.0	0.3	0.2
Large Green. halibut										
Small Green. halibut	0.3	0.5	0.0	0.8	0.3	0.0	0.0	0.0	0.0	0.0
American plaice	2.9	3.1	0.0	6.2	2.2	0.0	0.0	0.0	0.0	0.0
Flounders	1.9	1.0	1.1	3.0	1.2	0.0	0.0	0.0	0.0	0.0
Skates	0.2	0.2	0.0	0.4	0.2					
Redfish	11.8	4.3	8.0	16.4	14.1	0.0	0.0	0.0	0.0	0.0
Large demersals										
Small demersals	3.6	5.0	0.0	9.2	0.0	5.0	6.6	0.4	9.7	4.9
Capelin	30.3	37.4	4.0	73.1	56.5	18.3	3.8	15.6	20.9	20.7
Sand lance	0.0	0.1	0.0	0.1	0.0	0.6	0.8	0.0	1.1	1.1
Arctic cod	2.4	4.1	0.0	7.2	0.0	0.0	0.0	0.0	0.0	0.0
Large pelagics										
Pisci. small pelagics	13.8	23.6	0.0	41.1	1.3	0.0	0.0	0.0	0.0	0.0
Plank. small pelagics	6.9	4.1	2.1	9.3	2.1	0.0	0.0	0.0	0.0	0.0
Shrimp	4.0	1.6	2.2	5.3	2.2	15.4	8.1	9.7	21.1	9.9
Large crustacea	4.2	3.3	0.4	6.3	0.4	0.4	0.4	0.1	0.7	0.4
Echinoderms	2.6	2.1	0.6	4.7	2.7	0.1	0.2	0.0	0.2	0.1
Molluscs	1.0	0.9	0.4	2.0	1.3	0.1	0.0	0.1	0.1	0.1
Polychaetes	1.0	0.9	0.0	1.9	1.5	2.0	0.5	1.7	2.4	2.0
Other bent. inver.	0.3	0.2	0.0	0.5	0.3	0.2	0.2	0.0	0.3	0.2
Large zooplankton	10.3	14.4	1.2	26.9	8.8	56.9	5.9	52.8	61.1	59.0
Small zooplankton	0.1	0.1	0.0	0.1	0.1	0.9	0.8	0.3	1.4	1.4
Phytoplankton										
Detritus										
Total	100.0		20.8	220.2	100.0	100.0		80.6	119.4	100.0
TRN	20					19				

Greenland halibut

Background

Greenland halibut (*Reinhardtius hippoglossoides*) is a deep-water flatfish present in the North Atlantic and North Pacific. In the northwest Atlantic, they are found from Arctic regions to

Georges Bank (Bowering 1983). The Gulf of St. Lawrence population is considered to be a small stock, isolated from the main northwest Atlantic stock, completing its entire life cycle within the Gulf (DFO 2000a).

Directed fishing for this species with bottom trawls and gillnets developed after the mid-1970s. Catches increased in the 1980s to reach an all-time high in 1987 (11,000 t) but have since declined to around 3,000 t (Morin and Bernier 1993).

Greenland halibut were divided into large and small fish. Although there is an apparent change in diet composition when fish reach lengths of about 20 cm (Bundy et al. 2000), we separated Greenland halibut into fish larger or smaller than 40 cm, the size at which they are first recruited to the fishery (Brodie 1991). Greenland halibut greater than 40 cm in length are equivalent to fish aged six years and older (Brodie 1991).

Catch

According to NAFO fisheries statistics, the mean annual catch of large Greenland halibut during the 1985–1987 period was 2,642 tons or 2.54×10^{-2} t km^{-2} yr^{-1} (SD = 1.74×10^{-2} t km^{-2} yr^{-1}) (NAFO 1999). The inverse solution estimated a catch of 2.65×10^{-2} t km^{-2} yr^{-1}.

Since it was assumed that small Greenland halibut are not recruited to the fishery, and information on by-catch was not available for the northern Gulf area, catch in the model was set to zero for this group.

Biomass

Annual biomass estimates were obtained from groundfish survey data for the 1985–87 period (DFO, groundfish survey database, unpublished data). Length frequency data from each year were extrapolated to the whole northern Gulf area using the *PACES* software to obtain an estimate of halibut abundance for this zone. Total biomass was estimated each year by multiplying the abundance estimate for each length increment by mean mass at length (derived from length–mass relationships) and summing the results (Morin and Bernier 1993). This resulted in mean biomass estimates for the 1985–87 period of 28,261 t or 0.272 t km^{-2} (SD = 0.108 t km^{-2}) and 29,825 t or 0.287 t km^{-2} (SD = 0.130 t km^{-2}) for large (> 40 cm) and small ($\leq$ 40 cm) Greenland halibut, respectively.

Production

Due to the lack of reliable information on production (P) and total mortality (Z) of this species, it was assumed that production was equivalent to biomass multiplied by natural mortality (M) plus catch. Natural mortality for large Greenland halibut (M = 0.09) was estimated using FishBase (Froese and Pauly 2002) and a maximal length of 96.5 cm (the maximum length observed in samples during the 1985–1987 period) along with a water temperature of 3^{o}C. This resulted in a production of 0.050 t km^{-2} yr^{-1}. When the minimum and maximum biomass values were used, we obtained a production range of 0.017-0.095 t km^{-2} yr^{-1}. The inverse solution estimated a production of 0.063 t km^{-2} yr^{-1}, representing a P/B of 0.233 yr^{-1}.

For small Greenland halibut, it was assumed that natural mortality was higher (younger fish generally have a higher M than older fish), so a textbook value of 0.2 was assigned to this group. Since it was also assumed that there was no catch, this resulted in a production of 0.057 t km^{-2} yr^{-1}. When the minimum and maximum biomass values were used, we obtained a production range of 0.012 to 0.116 t km^{-2} yr^{-1}. The inverse solution estimated a production of 0.087 t km^{-2} yr^{-1}, representing a P/B of 0.303 yr^{-1}.

Consumption

A Q/B ratio was estimated using daily food requirements of 6- to 20-year-old Greenland halibut from the northwest Atlantic (Chumakov and Podrazhanskaya 1986). This resulted in a Q/B estimate of 1.660 yr^{-1} and a total consumption of 0.449 t km^{-2} yr^{-1} for large Greenland halibut. Another Q/B ratio was calculated using FishBase (Froese and Pauly 2002) for fish at 3°C and having a maximum mass of 9,217 g (DFO, groundfish survey database, unpublished data). This resulted in a Q/B value of 1.400 yr^{-1} and a consumption of 0.379 t km^{-2} yr^{-1}. Based on the previous mean production (0.050 t km^{-2} yr^{-1}) for large Greenland halibut and the minimum and maximum GE limits (10–30%), we obtained two other consumption values of 0.167 and 0.500 t km^{-2} yr^{-1}, respectively. However, assuming that this species would eat at least as much food as its biomass ($Q/B \geq 1$), we used 0.272 t km^{-2} yr^{-1} instead of 0.167 t km^{-2} yr^{-1}. The resulting lower and upper consumption limits were thus 0.272 and 0.500 t km^{-2} yr^{-1}, corresponding to a mean consumption of 0.386 ± 0.147 t km^{-2} yr^{-1}. The inverse solution estimated a consumption of 0.313 t km^{-2} yr^{-1}, representing a Q/B of 1.150 yr^{-1}.

Q/B values for small Greenland halibut were obtained from three different sources. Using the mean daily consumption of 5-year-old Greenland halibut (< 40 cm) (Chumakov and Podrazhanskaya 1986), Q/B and annual consumption were 4.427 yr^{-1} and 1.272 t km^{-2} yr^{-1}, respectively. Estimates obtained from FishBase (Froese and Pauly 2002), for fish at 3°C with a maximum mass of 586 g (the maximum mass of 40 cm fish from NAFO zones 4RS; DFO, groundfish survey database, unpublished data), were slightly lower, with Q/B and annual consumption values of 2.500 yr^{-1} and 0.718 t km^{-2} yr^{-1}. A third estimate (Q/B and annual consumption: 2.665 yr^{-1} and 0.766 t km^{-2} yr^{-1}) was obtained from a feeding study conducted in West Greenland (Pedersen and Riget 1992a), where we used the consumption values for fish smaller than 40 cm. Based on the previous mean production (0.057 t km^{-2} yr^{-1}) for small Greenland halibut and the minimum and maximum GE limits (10–30%), we obtained consumption values of 0.192 and 0.575 t km^{-2} yr^{-1}. However, assuming that this species would eat at least as much food as its biomass ($Q/B \geq 1$), we used 0.287 t km^{-2} yr^{-1} instead of 0.192 t km^{-2} yr^{-1}. The resulting lower and upper consumption limits were thus 0.287 and 1.272 t km^{-2} yr^{-1}, corresponding to a mean consumption of 0.780 ± 0.448 t km^{-2} yr^{-1}. The inverse solution estimated a consumption of 0.467 t km^{-2} yr^{-1}, representing a Q/B of 1.626 yr^{-1}.

Diet composition

Stomach content data for Greenland halibut from NAFO zones 4RS were not available for the 1985–1987 period. Diet data collected from 1993 to 2002 were assumed to be representative of the annual diet for the time period covered by the model. We used two periods: (1) 1994–1996, which represented the sampling period of the mid-1990 model and also included winter, spring, and summer samples; and (2) 1993 and 1997–2002, the other years (hereafter termed the "other-years" period) not accounted for in the mid-1990 model and which included spring and summer samples for large Greenland halibut and summer samples only for small Greenland halibut. Sampling was length-stratified and covered inshore and offshore zones for all seasons. In winter, inshore sampling was reduced due to ice cover. To estimate a diet most representative of the entire year, average diets were calculated for each season (in % mass) and then averaged into a final diet using the product "fullness index x season duration (in months)" as a weighting factor. Empty stomachs were included in the analysis for a better estimate of seasonal fluctuations in stomach fullness. Sample sizes for spring, summer, and winter, respectively, during the 1994–1996 period were 24, 1344, and 45 for large Greenland halibut and 30, 2446, and 25 for small Greenland halibut. The fullness indexes, including empty stomachs, were 0.38, 0.37, and 1.20 for spring, summer, and winter in large Greenland halibut and 2.31, 0.68, and 1.01 in small Greenland halibut. Sample sizes for spring and summer during the other-years period were 593 and 1881 for large Greenland halibut and the fullness indexes, including empty stomachs, were 0.12 and 0.37, respectively. For small Greenland halibut, sample size for summer during the other-years period was 5023 and the fullness indexes including empty stomachs was 0.54.

These two diets were used as constraints in inverse modelling (Table 9). The most important prey items of large Greenland halibut were capelin, shrimp, small planktonic pelagics, and small demersals (90.2% of the diet; Table 9). The most important prey items of small Greenland halibut were capelin, shrimp, and large zooplankton (90.2%; Table 9).

Table 9. Diet composition of large and small Greenland halibut used in modelling. Est: diet estimates by the inverse model; TRN: number of trophic relations; SD: standard deviation. All values are percentages except TRN. Empty cells indicate that a prey item was never found whereas "0.0" indicates that it was found in very small amounts.

	Large Greenland halibut (> 40 cm)					Small Greenland halibut (≤ 40 cm)				
Prey	Mean	± SD	Min	Max	Est	Mean	± SD	Min	Max	Est
Large cod										
Small cod	0.6	0.9	0.0	1.3	1.1	0.1	0.2	0.0	0.3	0.1
Large Green. halibut										
Small Green. halibut	0.5	0.7	0.1	1.0	0.8	0.1	0.2	0.0	0.3	0.1
American plaice	0.0	0.0	0.0	0.1	0.0					
Flounders	0.3	0.3	0.1	0.5	0.3	0.1	0.2	0.0	0.3	0.1
Skates	0.1	0.1	0.0	0.2	0.1					
Redfish	5.0	6.8	0.2	9.9	8.4	0.4	0.5	0.0	0.8	0.4
Large demersals										
Small demersals	15.9	12.4	7.2	24.7	15.7	6.5	5.9	2.3	10.6	5.4
Capelin	32.7	2.0	31.3	34.1	32.9	57.2	29.8	36.1	78.3	69.3
Sand lance	0.0	0.0	0.0	0.0	0.0	0.4	0.6	0.0	0.8	0.4
Arctic cod	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Large pelagics	0.0	0.0	0.0	0.0	0.0					
Pisci. small pelagics	1.6	1.6	0.5	2.7	2.2	2.0	1.3	1.1	2.9	2.0
Plank. small pelagics	16.6	12.6	7.7	25.5	14.9	0.0	0.0	0.0	0.0	0.0
Shrimp	25.0	6.6	20.3	29.7	22.0	18.6	13.1	9.3	27.9	9.9
Large crustacea	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Echinoderms	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Molluscs	0.0	0.0	0.0	0.0	0.0	0.1	0.1	0.0	0.2	0.1
Polychaetes	0.0	0.0	0.0	0.1	0.0	0.0	0.0	0.0	0.0	0.0
Other bent. inver.	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Large zooplankton	1.4	0.6	0.9	1.9	1.5	14.4	10.2	7.2	21.6	12.1
Small zooplankton	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.0	0.1	0.0
Phytoplankton										
Detritus										
Total	100.0		68.3	131.7	100.0	100.0		56.1	143.9	100.0
TRN	21					18				

American plaice, flounders, and skates

Background

The remaining flatfish were divided into three groups: American plaice (*Hippoglossoides platessoides*), flounders, and skates.

American plaice is widely distributed throughout the northwest Atlantic (from west Greenland to the Gulf of Maine) and is usually found at intermediate depths (80–250 m) (Morin et al. 1998). It has been exploited in NAFO zones 4RS since 1947, with commercial catches peaking in 1977. Annual catches then began to fall until the mid-1980s, when they levelled off at around 2,000 t, but yearly landings have since declined to around 1,000 t.

The flounder group consisted of witch flounder (*Glyptocephalus cynoglossus*), yellowtail flounder (*Limanda ferruginea*), fourspot flounder (*Paralichthys oblongus*), and winter flounder (*Pseudopleuronectes americanus*). Flounder were grouped together on the basis of their similar feeding behaviour. These four species are sedentary bottom-dwelling flatfish that live in relatively deep water, except for winter flounder, which lives mostly in infra-littoral waters. Their distribution ranges from the coast of Labrador in the north to North Carolina in the south. Since the 1950s, important commercial catches have occurred in the deep waters bordering the Laurentian Channel. A long-standing fishery has also been in place in shallower waters for winter flounder. The key species of the flounder group is witch flounder, mainly because of its high biomass and commercial significance, but also because there were no captures of the other species by the research surveys, which indicates that biomass was quite low. These other species are occasionally found in the stomachs of certain predators (e.g., seals). The thorny skate is widely distributed throughout the North Atlantic. The greatest concentrations are generally found in the higher part of continental shelves, at depths greater than 110 m (McEchran et al. 1976). The smooth skate is found throughout the northwest Atlantic, from the Gulf of St. Lawrence to Georges Bank (Scott and Scott 1988). Surveys conducted since the 1940s have shown that the greatest concentrations are found in the Gulf of St. Lawrence, on the Grand Banks of Newfoundland, and on the Scotian Shelf. This species lives at depths of 50 to 700 m but is mostly caught between 90 and 325 m (McKone and LeGrow 1983). Fishing activity is less important for the smooth skate than for the thorny skate.

The skate group included the two most abundant species of the *Rajidae* family in the study area: the thorny skate (*Raja radiata*), considered here as the key species for the group, and the smooth skate (*Raja senta*).

Catch

Prior to the mid 1980s, there was limited interest in commercial fishing of flounders and skates in NAFO zones 4RS. However, due to the cod fishery moratorium, fishing effort in this area has been redirected towards these species, witch flounder in particular. Catches of American plaice come mostly from by-catches in the cod and shrimp fisheries (Ouellet and Tremblay 1990), although a directed fishery occasionally takes place at the end of the season when cod fishermen have attained their quotas (Luciaà-Berdou et al. 1983). According to landing statistics (NAFO 1999), mean annual catch during the 1985–1987 period in NAFO zones 4RS was $2.04 \times 10^{-2} \pm 2.50 \times 10^{-3}$ t km^{-2} yr^{-1} for American plaice, $7.48 \times 10^{-3} \pm 1.08 \times 10^{-3}$ t km^{-2} yr^{-1} for witch flounder, and only $6.42 \times 10^{-5} \pm 7.36 \times 10^{-5}$ t km^{-2} yr^{-1} for skates. The inverse solution estimated catch values of 2.10×10^{-2}, 7.46×10^{-3}, and 6.84×10^{-5} t km^{-2} yr^{-1} for American plaice, flounders, and skates, respectively.

Biomass

Annual biomass estimates for the three groups were obtained using *PACES* to analyze research survey data from NAFO zones 4RS during the 1985–87 period (DFO, groundfish survey database, unpublished data). For flounders, mean biomass comprised witch flounder biomass, the only species for which data from the study area were available. Skate biomass was made up of both thorny and smooth skates. Mean biomass in NAFO zones 4RS during the 1985–1987 period was estimated at 69,189 t or 0.666 t km^{-2} (SD = 0.405 t km^{-2}) for American plaice, 36,347 t or 0.350 t km^{-2} (SD = 0.320 t km^{-2}) for flounders, and 17,301 t or 0.167 t km^{-2} (SD = 0.069 t km^{-2}) for skates.

Production

There was no information available on production or total mortality (Z) of American plaice, flounders, and skates within the study area. It was therefore assumed that for each group, production is equivalent to biomass multiplied by natural mortality, plus the catch. Natural mortality was assumed to be 0.220 yr^{-1} for American plaice (Pitt 1982) and 0.214 yr^{-1} for skates (Simon and Frank 1996). Due to a lack of information, natural mortality of flounders was simply assumed to be the textbook value of 0.200 yr^{-1}. Using this method, production estimates were 0.167, 0.077, and 0.036 t km^{-2} yr^{-1} for American plaice, flounders, and skates, respectively. When the minimum and maximum biomass values were used, we obtained production ranges of 0.066 to 0.406 t km^{-2} yr^{-1} for American plaice, 0.007 to 0.434 t km^{-2} yr^{-1} for flounders, and 0.021 to 0.054 t km^{-2} yr^{-1} for skates. Production values estimated by the inverse solution were 0.304 t km^{-2} yr^{-1} (P/B = 0.456 yr^{-1}) for American plaice, 0.177 t km^{-2} yr^{-1} (P/B = 0.507 yr^{-1}) for flounders, and 0.050 t km^{-2} yr^{-1} (P/B = 0.299 yr^{-1}) for skates.

Consumption

Consumption estimates for these three groups were derived from different sources. For all three groups, FishBase provided an initial Q/B estimate based on fish at 3°C (Froese and Pauly 2002). The Q/B and annual consumption values obtained in this way were 2.2 yr^{-1} and 1.466 t km^{-2} yr^{-1} for American plaice, 2.4 yr^{-1} and 0.840 t km^{-2} yr^{-1} for flounders (this value was the only one available for the group), and 1.5 yr^{-1} and 0.250 t km^{-2} yr^{-1} for skates.

For American plaice, a second estimate of consumption was derived from daily ration data using the model of Elliott and Persson (1978) with fish from the Newfoundland Grand Banks (Zamarro 1992). Mean daily consumption, calculated monthly, were 0.04% to 0.64% of body mass per day, with a final mean of 0.34%. Accordingly, the mean annual Q/B ratio and consumption were 1.241 yr^{-1} and 0.827 t km^{-2} yr^{-1}, respectively. A third study, with fish from Passamaquody Bay (New Brunswick), was used to determine consumption for American plaice (MacDonald and Waiwood 1987). The authors estimated food consumption to be 1.28% of body mass per day, resulting in a Q/B ratio of 4.672 yr^{-1} and a consumption of 3.114 t km^{-2} yr^{-1} (assuming that feeding is constant throughout the year). Based on the previous mean production (0.167 t km^{-2} yr^{-1}) for American plaice and the minimum and maximum GE limits (10–30%), we obtained consumption values of 0.557 and 1.670 t km^{-2} yr^{-1}. However, assuming that this species would eat at least as much food as its biomass ($Q/B \geq 1$), we used 0.666 t km^{-2} yr^{-1} instead of 0.557 t km^{-2} yr^{-1}. The resulting lower and upper consumption limits were thus 0.666 and 3.114 t km^{-2} yr^{-1}, corresponding to a mean consumption of 1.890 ± 1.150 t km^{-2} yr^{-1}. The inverse solution estimated a consumption of 1.953 t km^{-2} yr^{-1}, representing a Q/B of 2.930 yr^{-1}.

For the flounder group, the only available value was obtained from FishBase as described above. However, based on the previous mean production (0.077 t km^{-2} yr^{-1}) for flounders and the minimum and maximum GE limits (10–30%), we obtained consumption values of 0.258 and 0.775 t km^{-2} yr^{-1}. However, assuming that this species would eat at least as much food as its biomass ($Q/B \geq 1$), we used 0.350 t km^{-2} yr^{-1} instead of 0.258 t km^{-2} yr^{-1}. The resulting lower and upper consumption limits were thus 0.350 and 0.840 t km^{-2} yr^{-1}, corresponding to a mean consumption of 0.595 ± 0.319 t km^{-2} yr^{-1}. The inverse solution estimated a consumption of 0.678 t km^{-2} yr^{-1}, representing a Q/B of 1.936 yr^{-1}.

For skates, two other estimates of the Q/B ratio were taken into account. The first of these was determined for thorny skates from the Barents Sea (Dolgov 1997). Estimated annual consumption from this study was divided by mean biomass, resulting in an annual Q/B ratio and consumption of 2.369 yr^{-1} and 0.395 t km^{-2} yr^{-1} for our study area. The third estimate, based on thorny skate stomachs collected in the North Sea (Vinter 1989), produced a Q/B ratio and consumption estimate of 2.865 yr^{-1} and 0.477 t km^{-2} yr^{-1} for our study area. Based on the previous mean production (0.036 t km^{-2} yr^{-1}) for skates and the minimum and maximum GE limits (10–30%), we obtained consumption values of 0.119 and 0.357 t km^{-2} yr^{-1}. However, assuming that this species would eat at least as much food as its biomass ($Q/B \geq 1$), we used 0.167 t km^{-2} yr^{-1} instead of 0.119 t km^{-2} yr^{-1}. The resulting lower and upper consumption limits were thus 0.167 and 0.477 t km^{-2} yr^{-1}, corresponding to a mean consumption of 0.322 ± 0.153 t km^{-2} yr^{-1}. The inverse solution estimated a consumption of 0.277 t km^{-2} yr^{-1}, representing a Q/B of 1.665 yr^{-1}.

Diet composition

Diet data from NAFO zones 4RS during the 1985–1987 period were unavailable for all three groups, so studies from other areas and time periods were used instead. For American plaice, two studies provided some information on diet composition. In the first study, of 180 food-containing stomachs collected from bottom trawl survey cruises in western Nova Scotia from 1969 to 1972, primary prey items were echinoderms (60.4%) and large crustaceans (18.8%) (Langton and Bowman 1980). In the second study, based on 338 food-containing stomachs collected from the Flemish Cap bank during the summer of 1993, benthic species were the most important prey, including echinoderms (principally brittle stars; 86.4% by volume), large zooplankton such as hyperiids (10.9% by volume), and shrimp (1.0% by volume) (Rodriguez-Marin et al. 1994).

For flounders, very little diet information was available. The summer diet of witch flounder on the Flemish Cap bank was used and is principally made up of polychaetes (80.2% by volume), other benthic invertebrates (8.4% by volume), echinoderms (5.7% by volume), and bivalves (4.6% by volume) (Rodriguez-Marin et al. 1994).

The diet of the thorny skate was assumed to be representative of the entire skate group. Templeman (1982) examined the annual diet of thorny skates from the northwest Atlantic and found that the main prey species were (by volume) small demersal feeders (25.5%), redfish (23.6%), sand lance (15.8%), large crustaceans (14.3%), and small Atlantic cod (5.7%). A second study from the same area examined the diet composition of thorny skate from April 1969 to April 1970. Fish such as redfish, flounders, skates, small demersal feeders, and sand lance (each amounting to 10%) as well as invertebrates such as polychaetes (23.0%) and large crustaceans (18.9%) were the most important prey (by volume) in the skate diet (McEchran et al. 1976).

Due to the uncertainties with diet data, we also used the diet compositions for these three groups found by Bundy et al. (2000) in the Newfoundland–Labrador Shelf (1985–1987 period) to construct the upper and lower limits used to constrain values in inverse modelling (Table 10).

Table 10. Diet compositions of American plaice, flounders, and skates used in modelling. Est: diet estimates by the inverse model; TRN: number of trophic relations; SD: standard deviation. All values are percentages except TRN. Empty cells indicate that a prey item was never found whereas "0.0" indicates that it was found in very small amounts.

	American plaice					Flounders				
Prey	Mean	± SD	Min	Max	Est	Mean	± SD	Min	Max	Est
Large cod										
Small cod	0.2	0.3	0.0	0.5	0.2					
Large Green. halibut										
Small Green. halibut	0.3	0.5	0.0	0.8	0.3					
American plaice	0.9	1.5	0.0	2.1	1.0					
Flounders	0.4	0.6	0.0	0.9	0.3					
Skates										
Redfish	0.0	0.0	0.0	0.0	0.0					
Large demersals										
Small demersals	1.2	1.6	0.3	2.5	0.5	2.3	3.2	0.0	4.6	1.1
Capelin	15.2	24.8	0.0	35.1	21.5	2.4	3.3	0.0	4.7	3.2
Sand lance	6.6	10.7	0.0	15.1	12.6	2.4	3.4	0.0	4.9	4.2
Arctic cod	0.1	0.1	0.0	0.2	0.1					
Large pelagics										
Pisci. small pelagics	0.0	0.0	0.0	0.0	0.0					
Plank. small pelagics	0.0	0.0	0.0	0.1	0.0					
Shrimp	3.1	4.1	0.7	6.5	0.7	0.9	1.3	0.0	1.9	0.1
Large crustacea	8.1	13.2	0.0	18.8	1.6	0.2	0.3	0.0	0.5	0.2
Echinoderms	45.1	48.5	17.8	86.4	39.4	5.3	7.0	0.4	10.3	5.3
Molluscs	3.6	5.3	0.4	7.9	4.0	5.2	7.4	0.0	10.5	5.4
Polychaetes	3.6	4.7	0.8	7.5	4.7	50.2	42.1	20.6	80.1	50.4
Other bent. inver.	5.8	9.3	0.1	13.3	9.1	28.4	28.5	8.4	48.7	28.2
Large zooplankton	5.7	6.1	2.3	10.9	3.8	2.6	3.6	0.1	5.1	1.9
Small zooplankton	0.0	0.1	0.0	0.1	0.0	0.0	0.1	0.0	0.1	0.0
Phytoplankton										
Detritus										
Total	100.0		22.4	208.5	100.0	100.0		29.5	171.4	100.0
TRN	19					11				

Table 10. Cont.

	Skates				
Prey	Mean	± SD	Min	Max	Est
Large cod					
Small cod	2.8	4.4	0.0	6.2	4.7
Large Green. halibut					
Small Green. halibut	0.1	0.1	0.0	0.2	0.1
American plaice	0.1	0.1	0.0	0.2	0.1
Flounders	4.8	6.5	0.7	10.0	3.6
Skates	4.4	7.1	0.0	10.0	2.2
Redfish	14.3	10.6	8.6	23.6	19.0
Large demersals					
Small demersals	15.8	10.9	10.0	25.5	11.6
Capelin	4.4	7.1	0.0	10.0	3.0
Sand lance	12.5	5.8	10.0	18.2	15.5
Arctic cod	0.1	0.1	0.0	0.2	0.1
Large pelagics					
Pisci. small pelagics	3.2	5.1	0.0	7.2	3.6
Plank. small pelagics	0.4	0.7	0.0	0.9	0.2
Shrimp	1.3	1.0	0.8	2.2	1.1
Large crustacea	20.2	11.8	14.3	31.1	16.0
Echinoderms	0.9	1.3	0.1	2.0	0.9
Molluscs	1.3	0.8	0.8	2.0	1.4
Polychaetes	11.9	13.6	3.7	23.0	15.5
Other bent. inver.	0.6	0.9	0.0	1.3	0.7
Large zooplankton	1.0	1.3	0.2	2.0	0.8
Small zooplankton	0.1	0.1	0.0	0.1	0.1
Phytoplankton					
Detritus					
Total	100.0		49.4	175.8	100.0
TRN	20				

Redfish and demersal feeders

Background

The demersal feeders represent deep-water demersal species from NAFO zones 4RS. Because of its economic and ecological importance in the system, redfish was treated separately while the remaining demersal species were divided into large and small demersal feeders.

Redfish distribution in the northwest Atlantic ranges from west Greenland in the north to the Gulf of Maine in the south (Atkinson and Melteff 1987). Two redfish species are known to be the main component of the northwest Atlantic stock: *Sebastes mentella*, which generally occupies waters deeper than 250 m, and *Sebastes fasciatus*, usually found in shallower waters down to 300 m. Redfish usually inhabit waters from 100 to 700 m in depth and are ovoviviparous. Mating usually occurs in September or October, and females release live young from April to July. Redfish grow quite slowly, generally taking 8 to 10 years before being recruited to the commercial fishery at approximately 25 cm in length. This species has been commercially fished since the early 1950s, but catches have recently undergone important increases.

The large demersal feeders group is mainly made up of white hake (*Urophycis tenuis*), black dogfish (*Centroscyllium fabricii*), marlin spike grenadier (*Nezumia bairdi*), Atlantic halibut (*Hippoglossus hippoglossus*), wolffish (*Anarhichas* spp.), common lumpfish (*Cyclopterus lumpus*), haddock (*Melanogrammus aeglefinus*), longfin hake (*Urophycis chesteri*), large eelpout (Zoarcidae), monkfish (*Lophius americanus*), and grenadiers (Macrouridae). Information was very limited for most of these species in NAFO zones 4RS.

The small demersal feeders group includes sculpins (Cottidae), small eelpouts (Zoarcidae), fourbeard rockling (*Enchelyopus cimbrius*), cunner (*Tautogolabrus adspersus*), gunnels (Pholidae), lumpsuckers (*Eumicrotremus* sp.), and blennies (Stichaeidae). Juvenile of large demersal feeders were also considered as small demersal feeders. Unfortunately, little is known about these species and only scant information from the study area was available.

Catch

Commercial catch of redfish in NAFO zones 4RS during the 1985–87 period was taken from Morin and Bernier (1997) whereas total catch for the large demersal feeders group was calculated by summing NAFO landing statistics for each of the species listed above (NAFO 1999). Since there is no fishery for species in the small demersal feeders group and by-catch information was unavailable, catch was set at zero for this group. For redfish, the average annual catch was 27,486 t or 2.65×10^{-1} t km^{-2} yr^{-1} (SD = 2.56×10^{-2} t km^{-2} yr^{-1}). For the large demersal feeders, haddock and wolffish were the main species caught in 4RS during the 1985–87 period (68% of total landings). The average annual catch of the large demersal feeders was estimated at 962 tons or 9.26×10^{-3} t km^{-2} yr^{-1} (SD = 1.44×10^{-3} t km^{-2} yr^{-1}). The inverse solution estimated catch values of 2.64×10^{-1} and 9.21×10^{-3} t km^{-2} yr^{-1} for redfish and large demersal feeders, respectively.

Biomass

The *Lady Hammond* scientific survey provided data from NAFO zones 4RS during the 1985–87 period to estimate annual biomass (DFO, groundfish survey database, unpublished data). For redfish, length frequency data from each year were extrapolated to the whole northern Gulf area using the *PACES* software. Total biomass was estimated each year by multiplying the abundance estimate for each length increment by the mean mass at length (derived from length–mass relationships) and summing the results. For the large demersal feeders group, total biomass in the study area for each species was directly computed with *PACES* and results were summed.

Average annual biomass estimates were 1,261,248 t or 12.149 t km^{-2} (SD = 2.461 t km^{-2}) for redfish and 100,885 t or 0.972 t km^{-2} (SD = 0.171 t km^{-2}) for large demersal feeders.

Biomass for the small demersal feeders group was determined in the same way as for their large counterparts. Average annual biomass was estimated at 4,631 t or 0.045 t km^{-2} for the entire study area during the 1985–87 period. However, based on the solution developed by Bundy et al. (2000) for the Newfoundland–Labrador Shelf (1985–1987 period), the previous value seemed to be too low and was used as a lower limit. The upper limit was the mean (2.644 t km^{-2}) of the range (0.227 to 5.060 t km^{-2}) used by Bundy et al. (2000) in the Newfoundland ecosystem. A mean biomass of 1.343 ± 1.835 t km^{-2} was used here.

Production

Information on production and total mortality (Z) of redfish and large demersal species is lacking. Production was therefore assumed to be equivalent to biomass multiplied by natural mortality plus the catch (Allen 1971). Natural mortality (M) was assumed to be 0.125 yr^{-1} for redfish and 0.1 yr^{-1} for large demersal feeders. The lower value for large demersal feeders was chosen because this group contains species such as black dogfish and Atlantic halibut that are slow growing, long lived, and have relatively low natural mortality rates.

Production estimates were 1.783 and 0.106 t km^{-2} yr^{-1} for redfish and large demersal feeders, respectively. When the minimum and maximum biomass values were used, we obtained production ranges of 0.608 to 3.650 t km^{-2} yr^{-1} for redfish and 0.073 to 0.150 t km^{-2} yr^{-1} for large demersal feeders. Production values estimated by the inverse solution were 2.411 t km^{-2} yr^{-1} (P/B = 0.198 yr^{-1}) for redfish and 0.139 t km^{-2} yr^{-1} (P/B = 0.143 yr^{-1}) for large demersal feeders.

The same methodology was used for the small demersal feeders. Natural mortality was set to 0.330 yr^{-1}, the value estimated by FishBase for fourbeard rockling (the key species for the group) at a temperature of 3°C (Froese and Pauly 2002). A production value of 0.440 t km^{-2} yr^{-1} was estimated. When the minimum and maximum biomass values were used, we obtained a production range of 0.009 to 0.871 t km^{-2} yr^{-1}. The production value estimated by the inverse solution was 0.614 t km^{-2} yr^{-1} (P/B = 0.458 yr^{-1}) for small demersal feeders.

Consumption

FishBase was used to estimate the Q/B ratio of both redfish and large demersal feeders, assuming a water temperature of 3°C (Froese and Pauly 2002). This resulted in a Q/B of 2.1 yr^{-1} and a consumption value of 25.514 t km^{-2} yr^{-1} for redfish and a Q/B of 3.1 yr^{-1} and a consumption of 3.013 t km^{-2} yr^{-1} for the large demersal feeders.

Other information on redfish consumption is available. Dolgov and Revetnyak (1990) estimated annual food consumption to biomass ratios for Barents Sea deep-water redfish (*Sebastes mentella*) that varied from a high of 6.0 yr^{-1} for fingerlings down to around 1.3 yr^{-1} for fish of 19 years of age. Since fingerlings and very young fish did not make up a significant part of the biomass, the mean Q/B of fish from 10 to 19 years of age was computed. This produced a mean Q/B ratio of 1.490 yr^{-1} and an annual consumption of 18.103 t km^{-2} yr^{-1}. In another study on redfish from west Greenland, it was determined that daily rations were 0.46% and 0.86% of body mass for the autumn–winter and spring–summer periods, respectively (Pedersen and Riget 1992b). These two values were averaged, which gave a mean of 0.66% body mass per day and was equivalent to a Q/B ratio of 2.409 yr^{-1} and an annual consumption of 29.268 t km^{-2} yr^{-1}. On Georges Bank, the Q/B ratio for redfish was estimated at 7.970 yr^{-1}, which entailed a total consumption of 96.830 t km^{-2} yr^{-1} (Pauly 1989). Based on the previous mean production (1.783 t km^{-2} yr^{-1}) for redfish and the minimum and maximum GE limits (10–30%), we obtained consumption values of 5.945 and 17.834 t km^{-2} yr^{-1}. However, assuming that this species would eat at least as much food as its biomass ($Q/B \geq 1$), we used 12.149 t km^{-2} yr^{-1} instead of 5.945 t km^{-2} yr^{-1}. The resulting lower and upper consumption limits were 12.149 and 96.830 t km^{-2} yr^{-1}, corresponding to a mean consumption of 54.490 ± 41.821 t km^{-2} yr^{-1}. The inverse solution estimated a consumption of 13.123 t km^{-2} yr^{-1} for redfish, representing a Q/B of 1.080 yr^{-1}.

For the large demersal feeders, the only available value was obtained from FishBase as described above. Based on the previous mean production (0.106 t km^{-2} yr^{-1}) for large demersal feeders and the minimum and maximum GE limits (10–30%), we obtained consumption values of 0.355 and 1.064 t km^{-2} yr^{-1}. However, assuming that this species would eat at least as much food as its biomass ($Q/B \geq 1$), we used 0.972 t km^{-2} yr^{-1} instead of 0.355 t km^{-2} yr^{-1}. The resulting lower and upper consumption limits were 0.972 and 3.013 t km^{-2} yr^{-1}, corresponding to a mean consumption of 1.992 ± 1.376 t km^{-2} yr^{-1}. The inverse solution estimated a consumption of 1.133 t km^{-2} yr^{-1} for large demersal feeders, representing a Q/B of 1.166 yr^{-1}.

The only information available for the small demersal feeders were Q/B estimates computed from FishBase (Froese and Pauly 2002). We averaged the Q/B ratios obtained in this way for the two most abundant species of the group, fourbeard rockling and Atlantic soft pout, and obtained a mean Q/B ratio of 3.500 yr^{-1} and an annual consumption of 4.699 t km^{-2} yr^{-1}. To this value, we added the one used in Bundy et al. (2000) ($Q/B = 4.595$ yr^{-1} and $Q = 6.168$ t km^{-2} yr^{-1}). Based on the previous mean production (0.440 t km^{-2} yr^{-1}) for small demersal feeders and the minimum and maximum GE limits (10–30%), we obtained consumption values of 1.467 and 4.400 t km^{-2} yr^{-1}. The resulting lower and upper consumption limits were 1.467 and 6.168 t km^{-2} yr^{-1}, corresponding to a mean consumption of 3.817 ± 3.325 t km^{-2} yr^{-1}. The inverse solution estimated a consumption of 2.257 t km^{-2} yr^{-1} for small demersal feeders, representing a Q/B of 1.681 yr^{-1}.

Diet composition

Stomach content data for redfish were not available for the 1985–1987 period, so the 1993–1999 data were used to generate the annual diet composition for the time period covered by the model. We used two periods: (1) 1994–1996, which represented the sampling period of the mid-1990 model and also included winter, spring, and summer samples; and (2) 1993 and 1997–1999, the other years (hereafter termed the "other-years" period) not accounted for the mid-1990 model and which included spring and summer samples. Sampling was length-stratified and covered inshore and offshore zones for all seasons. In winter, inshore sampling was reduced due to ice cover. To estimate a diet most representative of the entire year, average diets were calculated for each season (in % mass) and then averaged into a final diet using sample size as a weighting factor. Empty stomachs were included in the analysis for a better estimate of seasonal fluctuations in stomach fullness. Sample sizes for spring, summer, and winter, respectively, during the 1994–

1996 period were 369, 1001, and 159. The fullness indexes, including empty stomachs, were 0.37, 0.54, and 0.96 for spring, summer, and winter, respectively. Sample sizes for spring and summer during the other-years period were 294 and 1493, and the fullness indexes, including empty stomachs, were 0.04 and 0.58, respectively. The most important prey items of redfish were shrimp, large zooplankton, and capelin for the 1994–1996 (94.2% of the diet) and other-years (97.2% of the diet) periods. The redfish diet from Bundy et al. (2000), in which main prey items were large zooplankton (53.8%), small zooplankton (16.1%), and small planktivorous pelagics (24.5%), was also used. The final diet compositions are shown in Table 11.

For large demersal feeders, diet was assumed to be that of white hake, the key species of the group. There was no diet information available for the Gulf of St. Lawrence, but some was found for the northeast United States and Scotian Shelf (Langton and Bowman 1980). In 169 white hake stomachs from these areas, small piscivorous pelagic feeders, small demersal feeders, and small planktivorous pelagic feeders were the most important prey items. We also used the diet composition estimated by Bundy et al. (2000) for this group.

There was no information found on the diet of small demersal feeders, so the diet estimated by Bundy et al. (2000) was used instead. The final diet compositions are shown in Table 11.

Table 11. Diet compositions of redfish, large demersal feeders, and small demersal feeders used in modelling. Est: diet estimates by the inverse model; TRN: number of trophic relations; SD: standard deviation. All values are percentages except TRN. Groups with indicated CV (available only as point estimates): Min = mean - (mean x 50%), Max = mean + (mean x 50%). Empty cells indicate that a prey item was never found whereas "0.0" indicates that it was found in very small amounts.

	Redfish					Large demersal feeders				
Prey	Mean	± SD	Min	Max	Est	Mean	± SD	Min	Max	Est
Large cod										
Small cod	0.1	0.1	0.0	0.2	0.0	3.8	3.9	1.1	6.6	6.2
Large Green. halibut										
Small Green. halibut						0.0	0.0	0.0	0.0	0.0
American plaice						0.8	1.2	0.0	1.7	1.3
Flounders						0.5	0.7	0.0	1.1	0.3
Skates						4.8	6.6	0.1	9.4	1.4
Redfish	1.1	1.7	0.0	2.4	2.4	3.2	2.3	1.6	4.8	4.2
Large demersals										
Small demersals	0.9	1.3	0.1	1.9	1.0	10.1	8.4	4.2	16.0	5.3
Capelin	10.3	14.4	0.7	21.1	21.1	6.7	3.9	3.9	9.4	7.6
Sand lance	0.7	1.0	0.0	1.4	1.4	6.1	4.7	2.7	9.4	8.6
Arctic cod						3.3	4.7	0.0	6.6	0.0
Large pelagics										
Pisci. small pelagics	0.3	0.4	0.0	0.5	0.2	8.2	11.4	0.1	16.2	10.2
Plank. small pelagics	11.5	17.3	0.0	24.5	1.2	6.8	4.9	3.4	10.3	3.4
Shrimp	31.1	41.7	3.5	62.4	3.9	7.5	2.2	5.9	9.0	6.0
Large crustacea						1.8	1.2	1.0	2.6	1.5
Echinoderms						10.0	14.1	0.0	19.9	12.4
Molluscs	0.0	0.0	0.0	0.0	0.0	3.3	4.7	0.0	6.7	5.1
Polychaetes	0.0	0.0	0.0	0.0	0.0	4.2	5.4	0.3	8.0	5.8
Other bent. inver.	0.0	0.0	0.0	0.0	0.0	7.3	9.6	0.5	14.1	10.7
Large zooplankton	36.3	21.7	23.1	53.8	52.7	10.9	10.8	3.3	18.5	9.2
Small zooplankton	7.8	11.1	0.4	16.1	16.1	0.8	0.8	0.2	1.4	0.9
Phytoplankton										
Detritus										
Total	100.0		27.8	184.3	100.0	100.0		28.2	171.8	100.0
TRN	13					20				

Table 11. Cont.

	Small demersal feeders (CV= 50%)				
Prey	Mean	± SD	Min	Max	Est
Large cod					
Small cod					
Large Green. halibut					
Small Green. halibut					
American plaice					
Flounders					
Skates					
Redfish					
Large demersals					
Small demersals	1.0		0.5	1.5	1.0
Capelin	2.0		1.0	3.0	1.8
Sand lance	1.0		0.5	1.5	1.0
Arctic cod	0.5		0.3	0.8	0.5
Large pelagics					
Pisci. small pelagics	0.2		0.1	0.3	0.2
Plank. small pelagics	0.3		0.2	0.5	0.3
Shrimp	2.0		1.0	3.0	1.0
Large crustacea	1.0		0.5	1.5	1.0
Echinoderms	10.0		5.0	15.0	8.9
Molluscs	10.0		5.0	15.0	9.1
Polychaetes	20.0		10.0	30.0	22.4
Other bent. inver.	42.0		21.0	63.0	45.1
Large zooplankton	5.0		2.5	7.5	3.4
Small zooplankton	5.0		2.5	7.5	4.3
Phytoplankton					
Detritus					
Total	100.0		50.0	150.0	100.0
TRN	14				

Forage fish

Background

There was very little information available on forage fish from NAFO zones 4RS. In most cases, data from other areas were used for the model. Four species were identified and separated into the following groups: capelin (*Mallotus villosus*), sand lance (*Ammodytes dubius* and *A. americanus*), and Arctic cod (*Boreogadus saida*).

Capelin is a small, short-lived pelagic fish that spends most of its life offshore, moving inshore only to spawn. The species is exploited commercially in some areas and is probably the most important forage fish of the northern Gulf of St. Lawrence.

Sand lance are small planktivorous semi-demersal fish found off the northwest Atlantic coast from Greenland to North Carolina (Nizinski et al. 1990). The northern sand lance (*Ammodytes dubius*) lives at water depths greater than 80 m, where water is colder, approximately 1°C. American sand lance (*Ammodytes americanus*) lives generally at depths of less than 20 m with temperatures around 6°C. Since the nearshore region (depths < 37 m) was not included in the model, the northern sand lance should be the most abundant species.

The Arctic cod has a circumpolar distribution and is found in the northwest Atlantic from arctic waters in the north down to the southern Gulf of St. Lawrence (Scott and Scott 1988). This species is pelagic and feeds mainly on invertebrates found in the upper part of the water column. Arctic cod is a key component of the marine food web of arctic waters (Hop et al. 1997) and an important link in the transfer of energy from zooplankton to other fish, marine mammals, and seabirds (Lilly et al. 1994).

Catch

The only species among the three groups that is commercially fished is capelin. There was no catch data entered in the model for sand lance or Arctic cod. For capelin, the average annual catch for the 1985–87 period in the study area was estimated from NAFO landing statistics to be 2,408 t or 2.32×10^{-2} t km^{-2} yr^{-1} (SD = 1.37×10^{-2} t km^{-2} yr^{-1}) (NAFO 1999). The inverse solution estimated a catch value of 2.45×10^{-2} t km^{-2} yr^{-1}.

Biomass

Annual biomass estimates of capelin were obtained from the *Lady Hammond* scientific surveys for the 1985–87 period using the *PACES* software (DFO, groundfish survey database, unpublished data). This resulted in a mean annual biomass estimate of 3,454,554 t or 33.277 t km^{-2} for the 4RS ecosystem. Since the biomass of this group was a gross approximation (the catchability for capelin is not very good with the fishing gear used by the groundfish survey), we also used an estimate (0.070 t km^{-2}) for the Lower St. Lawrence Estuary from acoustic surveys (Y. Simard, DFO, Institut Maurice-Lamontagne, Mont-Joli, Québec, personal communication). Taking the mean of these two values, capelin biomass was estimated to be 1,730,929 t or 16.674 t km^{-2} (SD = 23.481 t km^{-2}).

For sand lance, due to the lack of scientific research survey data or published information from the northern Gulf of St. Lawrence, biomass estimates were taken from Bundy et al. (2000). This biomass was estimated from research vessel surveys, which used a Campelen bottom trawl, and was adjusted by a catchability factor. The resulting mean annual biomass estimate was 248,889 t or 2.398 t km^{-2} (SD = 0.416 t km^{-2}) for NAFO zones 4RS.

For Arctic cod, it was assumed that the ratio between capelin and Arctic cod biomass is approximately 700:1 (M. Castonguay, personal communication), which gives an estimate of 1,038 t or 0.024 t km^{-2} (SD = 0.034 t km^{-2}).

Production

There was no information available concerning the P/B ratios in the study area for these three groups. For capelin, production was assumed to be equal to biomass multiplied by natural mortality plus the catch. Natural mortality was set to 0.6 yr^{-1} to better reflect the biology of this short-lived species (F. Grégoire, DFO, Institut Maurice-Lamontagne, Mont-Joli, Québec, personal communication). This produced an estimated P/B ratio and annual production of 0.601 yr^{-1} and 10.016 t km^{-2} yr^{-1}, respectively. When the minimum and maximum biomass values were used, we obtained a production range of 0.042 to 19.989 t km^{-2} yr^{-1}. The production value estimated by the inverse solution was 13.337 t km^{-2} yr^{-1} (P/B = 0.800 yr^{-1}) for capelin.

Due to the lack of information, the P/B ratio for sand lance was set to 1.150 yr^{-1} based on the model of Bundy et al. (2000), which represented an annual production of 2.757 t km^{-2} yr^{-1}. The production value estimated by the inverse solution was 2.930 t km^{-2} yr^{-1} (P/B = 1.222 yr^{-1}) for sand lance.

The P/B ratio (0.399 yr^{-1}) for Arctic cod was also taken from Bundy et al. (2000). We used the minimum and maximum biomass values to obtain a production range of 0.000 to 0.019 t km^{-2} yr^{-1}, corresponding to a mean production of 0.009 ± 0.013 t km^{-2} yr^{-1}. The production value estimated by the inverse solution was 0.016 t km^{-2} yr^{-1} (P/B = 0.665 yr^{-1}) for Arctic cod.

Consumption

Consumption rates for capelin, sand lance, and Arctic cod were taken from various sources. For all three species, the Q/B ratio was determined using FishBase (Froese and Pauly 2002). Q/B ratios for capelin and Arctic cod were estimated for a water temperature of 1°C, considering that these species are generally found near the cold intermediate layer in the Gulf of St. Lawrence. We obtained Q/B ratio values of 3.8 and 2.7 yr^{-1} for capelin and Arctic cod, respectively. For the two species of sand lance, the Q/B ratios estimated by FishBase at a temperature of 6°C for American sand lance and 1°C for northern sand lance were 5.0 and 8.5 yr^{-1}, respectively.

Other studies on the consumption of capelin were available. We used a second estimate based on the feeding ecology of capelin in the estuary and western Gulf of St. Lawrence (Vesin et al. 1981). The daily ration was estimated at 5.00% body mass in summer and 2.50% body mass in winter, giving a mean of 3.75% of body mass per day. From these values, the mean annual Q/B ratio was estimated to be 13.688 yr^{-1}. A third Q/B estimate was determined from a summer study on Barents Sea capelin (Ajiad and Pushaeva 1991). Daily ration was estimated to be between 1.47% and 2.00% of the body mass, resulting in an average Q/B ratio of 6.330 yr^{-1}. Finally, this resulted in a Q/B mean of 7.940 yr^{-1}. We used the minimum and maximum biomass values to obtain a consumption range of 0.559 to 264.220 t km^{-2} yr^{-1}, corresponding to a mean consumption of 132.389 ± 117.322 t km^{-2} yr^{-1}. The consumption values based on mean production and the minimum and maximum GE limits (10–30%) were included in this range. The consumption value estimated by the inverse solution was 57.076 t km^{-2} yr^{-1} (Q/B = 3.423 yr^{-1}) for capelin.

For sand lance, one other study conducted on Georges Bank from 1977 to 1986 was available (Gilman 1994). Daily rations (% body mass) of adults throughout the year were averaged, resulting in a mean Q/B ratio of 8.160 yr^{-1}. The overall mean Q/B ratio was 7.220 yr^{-1}, corresponding to a consumption of 17.310 t km^{-2} yr^{-1}. Based on the mean production (2.757 t km^{-2} yr^{-1}) for sand lance and the minimum and maximum GE limits (10–30%), we obtained consumption values of 9.190 and 27.571 t km^{-2} yr^{-1}. The resulting lower and upper consumption limits were 9.190 and 27.571 t km^{-2} yr^{-1}, corresponding to a mean consumption of 18.381 ± 12.997 t km^{-2} yr^{-1}. The inverse solution estimated a consumption of 14.693 t km^{-2} yr^{-1} for sand lance, representing a Q/B ratio of 6.129 yr^{-1}.

Finally, in addition to the FishBase value, a second Q/B ratio (3.941 yr^{-1}) was available for Arctic cod from Canadian arctic waters during 1988–90 (Hop et al. 1997). In this study, mean daily rations (% body mass per day) of juvenile and adult Arctic cod were estimated. The overall mean Q/B ratio was 3.321 yr^{-1}, corresponding to a consumption of 0.079 t km^{-2} yr^{-1}. Based on the mean production (0.009 t km^{-2} yr^{-1}) for Arctic cod and the minimum and maximum GE limits (10–30%), we obtained consumption values of 0.032 and 0.095 t km^{-2} yr^{-1}. The resulting lower and upper consumption limits were 0.032 and 0.095 t km^{-2} yr^{-1}, corresponding to a mean consumption of 0.063 ± 0.045 t km^{-2} yr^{-1}. The inverse solution estimated a consumption of 0.072 t km^{-2} yr^{-1} for Arctic cod, representing a Q/B ratio of 3.002 yr^{-1}.

Diet composition

For capelin, the diet compositions estimated by Bundy et al. (2000) for the Newfoundland–Labrador Shelf and Jangaard (1974) in the North Atlantic were used. Main prey items were copepods (*Temora longicornis*, *Calanus finmarchicus*, and *Pseudocalanus minutus*) and euphausiid eggs. We used also the study of Vesin et al. (1981) in the estuary and western Gulf of St. Lawrence. In that study, euphausiids and copepods were the main prey (59 and 41%, respectively). The final diet compositions are shown in Table 12.

The diet composition of sand lance was taken from Scott (1973), who examined fish caught on the Scotian Shelf. From a total of 130 stomachs, copepods, polychaete larvae, and euphausiids were the main prey items.

There was no diet data available for Arctic cod from the Gulf of St. Lawrence. Instead, a study on fish from the western Barents Sea (Lonne and Gulliksen 1989) and the diet composition estimated by Bundy et al. (2000) in the Newfoundland–Labrador Shelf were used to determine the resulting diet composition. Copepods and amphipods were the most important prey items found in Arctic cod stomachs. The final diet compositions are shown in Table 12.

Table 12. Diet compositions of capelin, sand lance, and Arctic cod used in modelling. Est: diet estimates by the inverse model; TRN: number of trophic relations; SD: standard deviation. All values are percentages except TRN. Groups with indicated CV (available only as point estimates): Min = mean - (mean x 50%), Max = mean + (mean x 50%). Empty cells indicate that a prey item was never found whereas "0.0" indicates that it was found in very small amounts.

	Capelin					Sand lance (CV= 50%)				
Prey	Mean	± SD	Min	Max	Est	Mean	± SD	Min	Max	Est
Large cod										
Small cod										
Large Green. halibut										
Small Green. halibut										
American plaice										
Flounders										
Skates										
Redfish										
Large demersals										
Small demersals										
Capelin	1.4	2.0	0.0	2.8	1.6					
Sand lance	1.4	2.0	0.0	2.8	2.6					
Arctic cod										
Large pelagics										
Pisci. small pelagics										
Plank. small pelagics										
Shrimp										
Large crustacea										
Echinoderms										
Molluscs										
Polychaetes										
Other bent. inver.	0.0	0.0	0.0	0.0	0.1	0.0		0.0	0.1	0.0
Large zooplankton	46.5	17.9	34.5	59.9	36.5	16.9		8.4	25.3	11.8
Small zooplankton	50.7	19.8	37.5	65.5	59.2	83.0		41.5	100.0	88.1
Phytoplankton						0.1		0.0	0.1	0.1
Detritus										
Total	100.0		72.0	131.0	100.0	100.0		50.0	125.4	100.0
TRN	5					4				

Table 12. Cont.

	Arctic cod				
Prey	Mean	± SD	Min	Max	Est
Large cod					
Small cod					
Large Green. halibut					
Small Green. halibut					
American plaice					
Flounders					
Skates					
Redfish					
Large demersals					
Small demersals					
Capelin	1.9	2.7	0.0	3.8	2.1
Sand lance					
Arctic cod	0.1	0.1	0.0	0.2	0.1
Large pelagics					
Pisci. small pelagics					
Plank. small pelagics					
Shrimp					
Large crustacea					
Echinoderms					
Molluscs					
Polychaetes					
Other bent. inver.					
Large zooplankton	34.4	41.8	4.8	64.0	37.8
Small zooplankton	63.6	44.7	32.0	95.2	60.0
Phytoplankton					
Detritus					
Total	100.0		36.8	163.2	100.0
TRN	4				

Pelagic feeders

Background

The pelagic feeders are also an important part of the ecosystem, and some species are commercially fished. Three boxes are designed to represent these species: large pelagic feeders, piscivorous small pelagic feeders, and planktivorous small pelagic feeders.

The large pelagic feeders group includes spiny dogfish (*Squalus acanthias*), pollock (*Pollachius virens*), and silver hake (*Merluccius bilinearis*). The most abundant large pelagic feeder in NAFO zones 4RS is silver hake, which was considered as the key species for the group. Juveniles of these species were classified as either piscivorous or planktivorous small pelagic feeders, according to juvenile feeding behaviour.

The piscivorous small pelagic feeders group includes Atlantic mackerel (*Scomber scombrus*) and short-finned squid (*Illex illecebrosus*). Mackerel populations in the northwest Atlantic form a complex stock that overwinters off the New England coast and then migrates northwards in May and June after spawning in the New Jersey Bight area and the southern Gulf of St. Lawrence (Moores et al. 1975). After spawning near the Îles-de-la-Madeleine, they disperse throughout the Gulf for the rest of the summer.

The planktivorous small pelagic feeders group includes Atlantic herring (*Clupea harengus*), Atlantic argentine (*Argentina silus*), planktivorous myctophids, and other mesopelagics. Atlantic herring, the only commercially fished species, is the most important in terms of biomass and was therefore considered the key species for the group. The spring-spawning population congregates off the Newfoundland west coast, in and around St. George Bay, while the autumn-spawning stock regroups further up the coast, north of Point Riche, to reproduce (McQuinn et al. 1999). Outside of the spawning season, these two stocks are mainly found in St. George Bay in the spring, north of Point Riche and in the Strait of Belle Isle in the summer, and off Bonne Bay in the fall, (McQuinn et al. 1999).

Catch

For the large pelagic feeders group, catch data for silver hake, pollock, and spiny dogfish (the only species for which data were available) were summed (NAFO 1999). Mean annual catch of large pelagic feeders in 1985–1987 was 259 t or 2.49×10^{-3} t km^{-2} yr^{-1} (SD = 2.22×10^{-3} t km^{-2} yr^{-1}). The inverse solution estimated a catch value of 2.66×10^{-3} t km^{-2} yr^{-1}.

Concerning piscivorous small pelagic feeders, catch data were only available for Atlantic mackerel. The mean catch in NAFO zones 4RS for 1985–87 was 1,297 t or 1.25×10^{-2} t km^{-2} yr^{-1} (SD = 1.71×10^{-2} t km^{-2} yr^{-1}) (Grégoire and Gilbert 1998). The inverse solution estimated a catch value of 1.38×10^{-2} t km^{-2} yr^{-1}.

Finally, for the planktivorous small pelagic feeders group, herring was the only species of the group for which catch statistics were available. The average catch in the study area during the 1985–87 period was 18,312 t or 1.76×10^{-1} t km^{-2} yr^{-1} (SD = 3.46×10^{-2} t km^{-2} yr^{-1}) (McQuinn et al. 1999). The inverse solution estimated a catch value of 1.77×10^{-1} t km^{-2} yr^{-1}.

Biomass

For the large pelagic feeders group, biomass was calculated from scientific research survey data covering NAFO zones 4RS during the 1985–1987 period. Biomass estimates were only available for silver hake, pollock, and spiny dogfish. Spiny dogfish, being a highly migratory species, was considered to be present in the study area for only six months of the year. Its biomass was therefore divided by half to compensate for the time spent outside NAFO zones 4RS. The biomasses of all three species were then summed to obtain an estimate for the group. The 1985–

1987 mean biomass for the large pelagic feeders group was estimated to be 6,167 t or 0.059 t km^{-2} (SD = 0.028 t km^{-2}).

Biomass estimates for Atlantic mackerel were derived from an egg production index calculated for 1983 to 1996 for the southern Gulf of St. Lawrence (F. Grégoire, unpublished data). We did not apply a residence time factor to reduce biomass by two (6 months outside the Gulf) because this kind of fish fed mainly during the summer period when they were in the Gulf. Only the 1985–1987 estimates were used to calculate the mean annual biomass. After spawning near the Îles-de-la-Madeleine, mackerel in the Gulf disperse throughout the entire area (NAFO zones 4RS and 4T). There is a little information about the proportion of mackerel that moves into the northern (4RS) versus southern (4T) Gulf. We assumed that one third of the biomass moved into 4RS while the other two thirds was distributed in 4T. Knowing that the northern Gulf represents 59.7% of the trawlable surface area of the entire Gulf of St. Lawrence, mackerel biomass was estimated to be 254,986 t or 2.456 t km^{-2}. The mean biomass for squid was estimated from scientific research survey data covering the 1985–1987 period to be 10 t or 0.0001 t km^{-2}. Total biomass for the piscivorous small pelagic feeders group in NAFO zones 4RS during 1985–1987 was estimated to be 406,937 tons or 2.456 t km^{-2} (SD = 0.851 t km^{-2}).

For the planktivorous small pelagic feeders group, the average biomass of herring (the key species for the group) during the 1985–87 period in the eastern part of the study area (NAFO zone 4R) was taken from the sequential population analysis (SPA) by McQuinn et al. (1999). Since herring populations in the western Gulf are considered to be small and data for this region were unavailable, it was assumed that the eastern Gulf population represented all the herring in the study area. The spring and autumn spawner biomasses were estimated at 170,037 and 84,934 t, respectively, for a total biomass of 254,971 t or 2.456 t km^{-2}. The biomass of Atlantic argentine in the study area, which was estimated from scientific research survey data, was 8,100 t or 0.078 t km^{-2} during the same period. Total biomass for the planktivorous small pelagic feeders group was 263,071 t or 2.534 t km^{-2} (SD = 0.070 t km^{-2}).

Production

Since there was no information on specific P/B ratios for these species in the study area, it was assumed that production was equal to biomass multiplied by natural mortality plus the catch. For the large pelagic feeders, natural mortality was assumed to be 0.1 because one of the principal species, spiny dogfish, is a large, long-living fish with a relatively low natural mortality (Scott and Scott 1988). For the piscivorous small pelagic feeders, in the absence of better information, the text book value of 0.2 was used for natural mortality. The same value, which was also used in the SPA, was used for the planktivorous small pelagic feeders (McQuinn et al. 1999). The resulting P/B ratios and production values were 0.142 yr^{-1} and 0.008 t km^{-2} yr^{-1} for the large pelagic feeders, 0.196 yr^{-1} and 0.481 t km^{-2} yr^{-1} for the piscivorous small pelagic feeders, and 0.270 yr^{-1} and 0.683 t km^{-2} yr^{-1} for the planktivorous small pelagic feeders. We created a range of production values by multiplying these P/B values by the minimum and maximum biomasses. This resulted in production ranges of 0.003 to 0.014 t km^{-2} yr^{-1} for large pelagic feeders, 0.335 to 0.676 t km^{-2} yr^{-1} for piscivorous small pelagics, and 0.630 to 0.744 t km^{-2} yr^{-1} for planktivorous small pelagics. The production values estimated by the inverse solution were 0.012 t km^{-2} yr^{-1} (P/B = 0.195 yr^{-1}) for the large pelagic feeders, 0.648 t km^{-2} yr^{-1} (P/B = 0.264 yr^{-1}) for the piscivorous small pelagic feeders, and 0.744 t km^{-2} yr^{-1} (P/B = 0.294 yr^{-1}) for the planktivorous small pelagic feeders.

Consumption

Consumption estimates for the three groups of pelagic feeders were available from different sources. For the large pelagic feeders, FishBase made available two Q/B estimates for silver hake (the key species for the group) from American waters (Froese and Pauly 2002). These values were 3.850 and 4.260 yr^{-1}, representing 0.253 and 0.229 t km^{-2} yr^{-1}, respectively. Three other consumption estimates were available for the large pelagic feeders group. Edwards and Bowman (1979) studied the food consumed by continental shelf fishes. A total of 17,000 stomachs obtained from 1963 to 1974 on the continental shelf between New Jersey and Halifax were analyzed. These authors estimated a Q/B ratio of 11.315 yr^{-1} or 0.672 t km^{-2} yr^{-1} for silver hake. In another study, Cohen and Grosselin (1981) examined food consumption of fish from Georges Bank. Silver hake consumption was estimated to be 0.452 t km^{-2} yr^{-1}, resulting in a Q/B of 7.605 yr^{-1}. The last source of information used comes from stomach content analysis and estimation of daily ration for silver hake (Durbin et al. 1983). A Q/B ratio of 7.869 yr^{-1} (or 0.467 t km^{-2} yr^{-1}) was estimated from this information. Based on the mean production (0.008 t km^{-2} yr^{-1}) for the large pelagic feeders and the minimum and maximum GE limits (10–30%), we obtained consumption values of 0.028 and 0.084 t km^{-2} yr^{-1}. However, assuming that this species would eat at least as much food as its biomass ($Q/B \geq 1$), we used 0.059 t km^{-2} yr^{-1} instead of 0.028 t km^{-2} yr^{-1}. The resulting lower and upper consumption limits were 0.059 and 0.672 t km^{-2} yr^{-1}, corresponding to a mean consumption of 0.366 ± 0.292 t km^{-2} yr^{-1}. The inverse solution estimated a consumption of 0.079 t km^{-2} yr^{-1} for the large pelagic feeders, representing a Q/B ratio of 1.335 yr^{-1}.

For the piscivorous small pelagic feeders, a Q/B estimate of 4.400 yr^{-1} for Atlantic mackerel, corresponding to an annual consumption of 10.807 t km^{-2} yr^{-1} (range: 7.361 to 14.795 t km^{-2} yr^{-1}) was taken from FishBase. Q/B information was also gathered from another source. Mehl and Westgard (1983) estimated mackerel consumption in the North Sea to be 6% of body mass per day (N=3,674). A Q/B ratio of 2.190 yr^{-1} (or 5.379 t km^{-2} yr^{-1}) was estimated from this information. Based on the mean production (0.481 t km^{-2} yr^{-1}) for the piscivorous small pelagic feeders and the minimum and maximum GE limits (10–30%), we obtained consumption values of 1.602 and 4.807 t km^{-2} yr^{-1}. However, assuming that this species would eat at least as much food as its biomass ($Q/B \geq 1$), we used 2.456 t km^{-2} yr^{-1} instead of 1.602 t km^{-2} yr^{-1}. The resulting lower and upper consumption limits were 2.456 and 14.795 t km^{-2} yr^{-1}, corresponding to a mean consumption of 8.626 ± 5.870 t km^{-2} yr^{-1}. The inverse solution estimated a consumption of 3.305 t km^{-2} yr^{-1} for the piscivorous small pelagic feeders, representing a Q/B ratio of 1.346 yr^{-1}.

For planktivorous small pelagics, Q/B estimates were derived from Pauly (1989), Rudstam et al. (1992), and Fetter and Davidjuka (1996). During summer, specific consumption rates of herring in the Baltic Sea were estimated to be from 10 to 20% of the body mass per day for young-of-the-year fish larger than 5 cm, 7 to 13% for 1+ fish, and 4 to 5% for older age groups. During autumn, these consumption rates declined to 2 to 4% for all age classes. This resulted in an estimated annual Q/B of 13.688 yr^{-1} and an annual consumption of 34.686 t km^{-2} yr^{-1}. Values taken from Pauly (1989) were 4.590 yr^{-1} and 11.632 t km^{-2} yr^{-1} for fish from Georges Bank and

10.100 yr^{-1} and 25.594 t km^{-2} yr^{-1} for fish from the North Sea. The final Q/B estimate used in the range comes from Fetter and Davidjuka (1996). Daily food consumption was calculated for different periods of the year. Mean values fluctuated widely between 0.2 and 1.3% of body mass per day, corresponding to an annual Q/B of 2.798 yr^{-1} and an annual consumption of 7.091 t km^{-2} yr^{-1}. Based on the mean production (0.683 t km^{-2} yr^{-1}) for the planktivorous small pelagic feeders and the minimum and maximum GE limits (10–30%), we obtained consumption values of 2.277 and 6.832 t km^{-2} yr^{-1}. However, assuming that this species would eat at least as much food as its biomass ($Q/B \geq 1$), we used 2.534 t km^{-2} yr^{-1} instead of 2.277 t km^{-2} yr^{-1}. The resulting lower and upper consumption limits were 2.534 and 34.686 t km^{-2} yr^{-1}, corresponding to a mean consumption of 18.610 ± 14.809 t km^{-2} yr^{-1}. The inverse solution estimated a consumption of 3.355 t km^{-2} yr^{-1} for the planktivorous small pelagic feeders, representing a Q/B ratio of 1.324 yr^{-1}.

Diet composition

The diet of the large pelagic feeders was assumed to be that of its key species, silver hake. Four sources of information were used. After analyzing a total of 498 silver hake digestive tracts, Bowman and Bowman (1980) found that three free-swimming crustaceans (i.e., *Crangon septemspinosa*, *Dichelopandalus leptocerus*, and *Monoculodes intermedius*) made up the largest part of the diet, accounting for 48% by mass. A second study examined the diet of 7,649 silver and red hake in the northwest Atlantic from 1965 to 1967 (Vinogradov 1983). In this study, the main prey items of silver hake were piscivorous small pelagics and euphausiids. On the Scotian Shelf, silver hake mainly preyed upon piscivorous small pelagic feeders and euphausiids (*M. norvegica*) (N = 2,855) (Waldron 1992). Finally, in another study on the Scotian Shelf, Langton and Bowman (1980) found that the main prey items of silver hake were euphausiids and Gadidae fish. The final diet composition is shown in Table 13.

Diet composition for the piscivorous small pelagic feeders were derived from two sources of information on Atlantic mackerel, the key species for this group. On the Scotian Shelf, the main prey in 199 mackerel stomachs were hyperid amphipods, euphausiids, and fish larvae (mainly blennoids and gadoids) (Kulka and Stobo 1981). The other diet study examined 359 stomachs of mackerel from the Gulf of St. Lawrence and the Scotian Shelf (Grégoire and Castonguay 1989). In this study, the main prey species (in % abundance) were found to be nematodes (which were probably stomach parasites), copepods, and unidentified larvae. Combining these two diets, large zooplankton, small zooplankton, and capelin were the most important prey (Table 13).

For the diet of the planktivorous small pelagics group, we used the diet composition estimated by Bundy et al. (2000) in the Newfoundland–Labrador Shelf and the stomach content data available from NAFO zones 4T (M. Hanson, DFO, Gulf Fisheries Centre, New Brunswick, unpublished data) (Table 13).

Table 13. Diet compositions of large pelagic feeders, piscivorous small pelagic feeders, and planktivorous small pelagic feeders used in modelling. Est: diet estimates by the inverse model; TRN: number of trophic relations; SD: standard deviation. All values are percentages except TRN. Empty cells indicate that a prey item was never found whereas "0.0" indicates that it was found in very small amounts.

	Large pelagic feeders					Piscivorous small pelagic feeders				
Prey	Mean	± SD	Min	Max	Est	Mean	± SD	Min	Max	Est
Large cod										
Small cod	4.5	9.2	0.0	12.9	8.7	0.0	0.0	0.0	0.0	0.0
Large Green. halibut										
Small Green. halibut										
American plaice	0.0		0.0	0.0	0.0					
Flounders	0.1	0.1	0.0	0.2	0.1					
Skates	0.8	1.7	0.0	2.3	1.1					
Redfish	0.1	0.2	0.0	0.3	0.1					
Large demersals										
Small demersals	5.3	10.8	0.0	15.3	2.2	0.0	0.0	0.0	0.0	0.0
Capelin	3.5	7.1	0.0	10.0	6.7	0.0	0.0	0.0	0.0	0.0
Sand lance	4.2	8.6	0.0	12.2	10.4	0.0	0.0	0.0	0.0	0.0
Arctic cod	4.5	9.2	0.0	12.9	0.0	0.0	0.0	0.0	0.0	0.0
Large pelagics										
Pisci. small pelagics	23.7	45.1	2.2	66.0	39.3					
Plank. small pelagics	7.1	14.5	0.0	20.5	3.8	0.0	0.0	0.0	0.0	0.0
Shrimp	24.1	48.7	0.3	69.1	4.0	0.2	0.3	0.0	0.4	0.2
Large crustacea	0.0	0.1	0.0	0.1	0.0					
Echinoderms	0.8	1.6	0.0	2.3	1.1					
Molluscs						0.2	0.3	0.0	0.4	0.2
Polychaetes	0.2	0.4	0.0	0.5	0.2					
Other bent. inver.	8.1	16.5	0.0	23.3	13.8					
Large zooplankton	12.5	19.2	4.5	31.6	7.4	54.2	64.1	8.9	99.6	22.1
Small zooplankton	0.6	1.3	0.0	1.8	1.1	45.5	64.4	0.0	91.1	77.5
Phytoplankton										
Detritus										
Total	100.0		7.1	281.4	100.0	100.0		8.9	191.4	100.0
TRN	18					10				

Table 13. Cont.

	Planktivorous small pelagic feeders				
Prey	Mean	± SD	Min	Max	Est
Large cod					
Small cod					
Large Green. halibut					
Small Green. halibut					
American plaice					
Flounders					
Skates					
Redfish					
Large demersals					
Small demersals					
Capelin					
Sand lance					
Arctic cod					
Large pelagics					
Pisci. small pelagics					
Plank. small pelagics					
Shrimp	6.3	9.7	0.0	13.7	0.0
Large crustacea					
Echinoderms					
Molluscs					
Polychaetes					
Other bent. inver.	4.6	7.1	0.0	10.0	6.3
Large zooplankton	43.1	66.2	0.0	93.7	9.9
Small zooplankton	46.0	70.7	0.0	100.0	83.7
Phytoplankton					
Detritus					
Total	100.0		0.0	217.4	100.0
TRN	4				

Crustaceans

Background

The main crustaceans of the northern Gulf of St. Lawrence ecosystem are shrimp and snow crab. Both are exploited commercially.

The shrimp group consists of several species of penaeid and caridean shrimp and is represented by the key species northern shrimp, *Pandalus borealis*, which dominates the biomass and is fished commercially. Generally, shrimp are found throughout the Estuary and the northern

Gulf of St. Lawrence at depths of 150–350 m, but migrations do occur during breeding (the females migrate to shallower waters at the channel heads) and feeding (at night, they leave the ocean floor to feed on small planktonic organisms) (DFO 2000b).

The snow crab (*Chionoecetes opilio*) represents the key species of the large crustacean group, which also includes other non-commercial species such as toad crabs (*Hyas* spp.). Other crustaceans such as the American lobster (*Homarus americanus*) were not included in the model because they are found mainly in the infra-littoral zone. This zone was excluded from the model because exchanges between infra-littoral and pelagic zones are still poorly understood (A. Vézina, DFO, Bedford Institute of Oceanography, Nova Scotia, personal communication). Snow crab is highly exploited in the northern Gulf of St. Lawrence, particularly along Québec's North Shore.

Catch

Information on commercial landings of northern shrimp are available since 1982 for the three management units in the northern Gulf: Sept-Îles, Anticosti, and Esquiman (Savard 1999). The mean of annual landings from 1985 to 1987 is 9,757 t, resulting in a total catch of 9.40×10^{-2} t km^{-2} yr^{-1} (SD = 1.49×10^{-2} t km^{-2} yr^{-1}). The inverse solution estimated a catch value of 9.07×10^{-2} t km^{-2} yr^{-1}.

For snow crab, a mean of 4,557 t was taken annually between 1985 and 1987, resulting in a total catch of 4.39×10^{-2} t km^{-2} yr^{-1} (SD = 3.33×10^{-3} t km^{-2} yr^{-1}) (Dufour 1995). The inverse solution estimated a catch value of 4.41×10^{-2} t km^{-2} yr^{-1}.

Biomass

Shrimp biomass for the northern Gulf was derived from estimates for the three management units in this area (Savard and Hurtubise 1991). Mean biomass over the 1985–87 period was 86,210 t or 0.830 t km^{-2} (SD = 0.561 t km^{-2}).

Current snow crab assessments do not estimate the total biomass in the Gulf of St. Lawrence. Biomass for this group was estimated using CPUE data for the period 1985–1987. Using the Leslie method (Leslie and Davis 1939), we can obtain the biomass of snow crab available to fishing gear. These data do not include females or immature males that are too small and avoid capture. However, from 1989 to 1998, a complete bottom trawl survey was conducted in the baie Sainte-Marguerite (B. Sainte-Marie, DFO, Institut Maurice-Lamontagne, Mont-Joli, Québec, personal communication). Using these data, a ratio of commercial biomass to non-commercial biomass was computed. Assuming that size structure is the same throughout the Gulf, this ratio was used to transform the commercial biomass estimated with CPUEs to total biomass estimates. In this way, we obtained a mean biomass estimate of 89,500 t or 0.862 t km^{-2} (SD = 0.204 t km^{-2}) for the 1985–1987 period.

Production

Due to the lack of information, the range of P/B ratios for shrimp was set to 1.450 yr^{-1} based on the model of Bundy et al. (2000). Multiplying this value by the minimum and maximum biomass values for shrimp, we estimated a production range between 0.838 and 1.570 t km^{-2} yr^{-1}, corresponding to an annual production of 1.204 ± 0.517 t km^{-2} yr^{-1}. The inverse solution estimated a production of 1.449 t km^{-2} yr^{-1}, representing a P/B of 1.744 yr^{-1}.

For snow crab, an assumed natural mortality of 0.2 yr^{-1} was used to take into account the high natural mortality of juveniles as well as the lower natural mortality of adults (B. Sainte-Marie, personal communication). This produced a P/B ratio of 0.251 yr^{-1}. To obtain a range, we multiplied this P/B value by the minimum and maximum biomasses, and this resulted in productions ranging from 0.114 to 0.475 t km^{-2} yr^{-1}, corresponding to an annual production of 0.216 ± 0.255 t km^{-2} yr^{-1}. The inverse solution estimated a production of 0.289 t km^{-2} yr^{-1}, representing a P/B of 0.335 yr^{-1}.

Consumption

In the absence of information on food consumption by northern shrimp, consumption was only estimated by using the gross growth efficiency (GE, the ratio of production to consumption). Based on the mean production (1.204 t km^{-2} yr^{-1}) for shrimp and the minimum and maximum GE limits (10–30%), we obtained two consumption values of 4.014 and 12.041 t km^{-2} yr^{-1}, corresponding to a mean consumption of 8.028 ± 5.676 t km^{-2} yr^{-1}. The inverse solution estimated a consumption of 5.970 t km^{-2} yr^{-1} for shrimp, representing a Q/B ratio of 7.189 yr^{-1}.

Snow crab consumption data were obtained from a study conducted in the baie des Chaleurs and the southern Gulf of St. Lawrence (Brêthes et al. 1984). A daily ration of 0.4% of body mass was estimated, resulting in a Q/B ratio of 1.460 yr^{-1} (or 1.259 t km^{-2} yr^{-1}). A second estimate was derived from a study of the physiological energetics of the snow crab (Thompson and Hawryluk 1990). The estimated Q/B ratio was 1.302 yr^{-1} (or 1.122 t km^{-2} yr^{-1}). Based on the mean production (0.216 t km^{-2} yr^{-1}) for large crustaceans and the minimum and maximum GE limits (10–30%), we obtained two other consumption values of 0.721 and 2.163 t km^{-2} yr^{-1}. The resulting lower and upper consumption limits were 0.721 and 2.163 t km^{-2} yr^{-1}, corresponding to a mean consumption of 1.442 ± 0.609 t km^{-2} yr^{-1}. The inverse solution estimated a consumption of 1.224 t km^{-2} yr^{-1} for large crustaceans, representing a Q/B ratio of 1.420 yr^{-1}.

Diet composition

For shrimp, feeding occurs in both the benthic and pelagic environments, in accordance with their daily vertical migrations. In their model, Bundy et al. (2000) assumed that 30% of the total diet is benthic and 70% is pelagic. Annelids, small crustaceans, detritus, and bottom plants were the main prey during the day while copepods and euphausiids were the principal prey items during the nocturnal migration (Table 14).

For snow crab, diet data were available from the baie des Chaleurs and the southern Gulf of St. Lawrence (Brêthes et al. 1984) as well as the west coast of Newfoundland (Wieczorek and

Hooper 1995). From the study by Brêthes et al. (1984), abundance estimates were multiplied by the mean mass of each prey to obtain biomass indices for the diet. The main prey items of the 480 snow crabs were decapods, polychaetes, and gastropods. In the study of Wieczorek and Hooper (1995) (N = 198 stomachs), the main components of the diet in terms of mass were annelids, echinoderms, and molluscs such as bivalves. We also used the diet composition estimated by Bundy et al. (2000) in the Newfoundland–Labrador Shelf, where the main prey were annelids, echinoderms, and molluscs. The final diet composition for this group is shown in Table 14.

Table 14. Diet compositions of shrimp and large crustacea used in modelling. Est: diet estimates by the inverse model; TRN: number of trophic relations; SD: standard deviation. All values are percentages except TRN. Groups with indicated CV (available only as point estimates): Min = mean - (mean x 50%), Max = mean + (mean x 50%). Empty cells indicate that a prey item was never found whereas "0.0" indicates that it was found in very small amounts.

	Shrimp (CV= 50%)					Large crustacea				
Prey	Mean	± SD	Min	Max	Est	Mean	± SD	Min	Max	Est
Large cod										
Small cod										
Large Green. halibut										
Small Green. halibut										
American plaice										
Flounders										
Skates										
Redfish										
Large demersals										
Small demersals						1.8	3.5	0.0	5.0	0.8
Capelin										
Sand lance										
Arctic cod										
Large pelagics										
Pisci. small pelagics										
Plank. small pelagics										
Shrimp	0.0		0.0	0.0	0.0	1.8	3.3	0.2	4.9	0.3
Large crustacea						4.0	7.8	0.0	11.1	0.3
Echinoderms						11.8	22.3	0.5	32.1	16.4
Molluscs						26.9	46.1	4.8	69.9	18.9
Polychaetes	1.5		0.8	2.3	1.5	16.0	23.6	5.5	38.8	18.1
Other bent. inver.	1.5		0.8	2.3	1.8	17.9	35.0	0.1	49.6	28.0
Large zooplankton	12.0		6.0	18.0	9.1	14.4	27.6	0.4	39.4	11.0
Small zooplankton	24.0		12.0	36.0	24.1	1.8	3.4	0.1	4.9	1.9
Phytoplankton	8.5		4.3	12.8	9.7	0.0	0.0	0.0	0.0	0.0
Detritus	52.5		26.3	78.8	53.8	3.6	7.1	0.0	10.0	4.2
Total	100.0		50.0	150.0	100.0	100.0		11.5	265.8	100.0
TRN	7					11				

Benthic invertebrates

Background

The benthic invertebrates were divided into four groups: echinoderms, molluscs, polychaetes, and other benthic invertebrates. This last group consisted mainly of miscellaneous crustaceans, nematodes, and other meiofauna. Benthic data for the northern Gulf of St. Lawrence were lacking. Consequently, in many cases it was assumed that benthic biomass was similar to that of the Newfoundland–Labrador Shelf ecosystem (Bundy et al. 2000). The most recent comprehensive source of information on the benthos is a study carried out in 1980 under the auspices of the Mobil Oil Company on the Grand Banks of Newfoundland (Hutcheson et al. 1981).

For all the molluscs considered in the ecosystem, only part of the biomass, the soft body tissue, is transferred through the food web. This is confirmed by observations of huge shells beds on the ocean floor (Hutcheson et al. 1981). In order to reduce the biomass and account for soft body tissue only, the ratio of the body mass to whole mass of the mollusc *Mesodesma deauratum* was estimated. The mean ratio between blotted wet mass of tissue to whole mass for animals with a shell length between 30 and 35 mm was 0.166 ± 0.023 (N = 10, K. Gilkinson, DFO, Northwest Atlantic Fisheries Centre, White Hills, St. John's, Newfoundland, unpublished data).

Catch

Polychaetes, echinoderms, and other benthic invertebrates were not exploited commercially in the study area during the 1985–1987 period. Only molluscs were commercially harvested. Commercial species are soft-shelled clams (*Mya arenaria*), sea scallops (*Placopecten magellanicus*), whelks (*Busycon* sp.), and periwinkles (*Littorina* sp.). Average annual landings were taken from NAFO statistics and are 3,462 t or 3.34 x 10^{-2} t km^{-2} yr^{-1} (SD = 4.10 x 10^{-3} t km^{-2} yr^{-1}) (NAFO 1999). The inverse solution estimated a catch value of 3.34 x 10^{-2} t km^{-2} yr^{-1}. However, these different values were for the whole mass including the shell. The uncorrected catch estimate represented only 0.1% of total production estimate of molluscs (or total mortality). Consequently, a decrease in this value after correcting for soft body tissue should not have a large impact on the modelling results.

Biomass

The mean biomasses for 4RS were assumed to be the same as for 2J3KLNO and were 112.300 t km^{-2} for echinoderms, 42.100 t km^{-2} for molluscs, 10.500 t km^{-2} for polychaetes, and 7.800 t km^{-2} for other benthic invertebrates.

Production

There is no information available on P/B ratios of benthic invertebrates in the northern Gulf. All the estimates are taken from the literature for other areas.

Echinoderms

Warwick et al. (1978) estimated an annual production of 0.23 t km^{-2} yr^{-1} for echinoderms in Carmarthen Bay (South Wales, U.K.) while Buchanan and Warwick (1974) made an estimate of 0.11 t km^{-2} yr^{-1}. However, higher echinoderm productions have been reported in the New York Bight (70.11 t km^{-2} yr^{-1}, Steimle 1985) and in Georges Bank (64.22 t km^{-2} yr^{-1}, Steimle 1987). Production could range between 0.108 and 70.108 t km^{-2} yr^{-1}, corresponding to an annual production of 33.667 ± 38.755 t km^{-2} yr^{-1}. The inverse solution estimated a production of 36.257 t km^{-2} yr^{-1}, representing a P/B of 0.323 yr^{-1}.

Molluscs

For molluscs, Warwick et al. (1978) estimated an annual production of 3.820 t km^{-2} yr^{-1} in Carmarthen Bay (South Wales, U.K.) while Sanders (1956) estimated 4.670 t km^{-2} yr^{-1} in Long Island Sound. Higher production estimates were reported by Steimle (1985) (82.121 t km^{-2} yr^{-1} for a P/B of 1.951 yr^{-1}) and by Borkowski (1974) (23.530 t km^{-2} yr^{-1} for a P/B of 0.559 yr^{-1}), as well as lower estimates such as 0.600 t km^{-2} yr^{-1} (P/B of 0.014 yr^{-1}) in Buchanan and Warwick (1974). Production could thus range between 0.600 and 82.121 t km^{-2} yr^{-1}, corresponding to an annual production of 22.949 ± 34.282 t km^{-2} yr^{-1}. The inverse solution estimated a production of 39.278 t km^{-2} yr^{-1}, representing a P/B of 0.933 yr^{-1}.

Polychaetes

Estimates of the annual production of polychaetes ranged between 0.206 and 74.564 t km^{-2} yr^{-1} (0.206 t km^{-2} yr^{-1} in Buchanan and Warwick [1974], 0.940 t km^{-2} yr^{-1} in Warwick et al. [1978], 5.520 t km^{-2} yr^{-1} in Sanders [1956], 6.310 t km^{-2} yr^{-1} in Collie [1987], 8.250 t km^{-2} yr^{-1} in Peer [1970], 16.050 t km^{-2} yr^{-1} in Nichols [1975], 21.600 t km^{-2} yr^{-1} in Curtis [1977], and 74.564 t km^{-2} yr^{-1} in Steimle [1985]). This represented an annual production of 16.680 ± 27.487 t km^{-2} yr^{-1}. The inverse solution estimated a production of 26.750 t km^{-2} yr^{-1}, representing a P/B of 2.548 yr^{-1}.

Other benthic invertebrates

Estimates of annual production for other benthic invertebrates ranged between 0.517 and 15.677 t km^{-2} yr^{-1} (0.517 t km^{-2} yr^{-1} in Sheader [1977], 5.000 t km^{-2} yr^{-1} in Klein et al. [1975], 15.500 t km^{-2} yr^{-1} in Cederwall [1977], and 15.677 t km^{-2} yr^{-1} in Collie [1985]). This represented an annual production of 9.173 ± 7.631 t km^{-2} yr^{-1}. The inverse solution estimated a production of 9.172 t km^{-2} yr^{-1}, representing a P/B of 1.176 yr^{-1}.

Consumption

In the absence of information on food consumption, consumption values were estimated by taking gross growth efficiency (GE) between 0.09 and 0.30 (Christensen and Pauly 1992a). For echinoderms, this produced a consumption range between 112.222 and 374.072 t km^{-2} yr^{-1}, corresponding to a mean consumption of 243.147 ± 185.156 t km^{-2} yr^{-1}. The inverse solution estimated a consumption of 190.634 t km^{-2} yr^{-1}, representing a Q/B ratio of 1.698 yr^{-1}.

For molluscs, this produced a consumption range between 76.497 and 254.991 t km^{-2} yr^{-1}, corresponding to a mean consumption of 165.744 ± 126.214 t km^{-2} yr^{-1}. The inverse solution estimated a consumption of 171.020 t km^{-2} yr^{-1}, representing a Q/B ratio of 4.062 yr^{-1}.

For polychaetes, this produced a consumption range between 55.601 and 185.336 t km^{-2} yr^{-1}, corresponding to a mean consumption of 120.468 ± 91.737 t km^{-2} yr^{-1}. The inverse solution estimated a consumption of 113.794 t km^{-2} yr^{-1}, representing a Q/B ratio of 10.838 yr^{-1}.

For other benthic invertebrates, this produced a consumption range between 30.578 and 101.926 t km^{-2} yr^{-1}, corresponding to a mean consumption of 66.252 ± 50.451 t km^{-2} yr^{-1}. The inverse solution estimated a consumption of 48.485 t km^{-2} yr^{-1}, representing a Q/B ratio of 6.216 yr^{-1}.

Diet composition

Diet information for these groups was taken from Bundy et al. (2000), where much of the data originates from the works of Nesis (1965) and Hutcheson et al. (1981).

For echinoderms, diet information was taken from the three most abundant species in NAFO zones 2J3KL: the sand dollar (*Echinarchnius parma*) the sea urchin (*Strongylocentrotus pallidus*), and the brittle star (*Ophiura robusta*). The resulting diet is 100% detritus (Bundy et al. 2000).

For molluscs, Bundy et al. (2000) analyzed the diet composition of a suspension feeder (*Macoma deauratum*), a deposit feeder (*Macoma calcarea*), and a suspension or detrital feeder (*Liocyma fluctuosa*). Suspension feeders feed on organic detrital matter that is resuspended in the water immediately above the sediment surface. Deposit feeders can be considered as detrital feeders. Thus, the molluscs are assumed to be detrital feeders of various forms and the diet of the mollusc group is 100% detritus. However, in shallower waters, molluscs could consume phytoplankton (M. Fréchette, DFO, Institut Maurice-Lamontagne, Mont-Joli, Québec, personal communication). This potential food was also accounted for in the final diet composition (Table 15).

The polychaetes are considered to have a diet of 100% detritus (Nesis 1965; Fauchald and Jumars 1979). However, recent studies at two deeper Laurentian trough stations (275 and 325 m depth) showed that polychaetes could also consume phytoplankton and that cannibalism could have a significant impact in the diet composition (Desrosiers et al. 2000). The resulting diet is shown in Table 15.

The key organisms for the other benthic invertebrates group are gammarid amphipods. These species feed mainly on organic detritus (Nesis 1965; Hutcheson et al. 1981).

Table 15. Diet compositions of molluscs and polychaetes used in modelling. Est: diet estimates by the inverse model; TRN: number of trophic relations; SD: standard deviation. All values are percentages except TRN. Empty cells indicate that a prey item was never found whereas "0.0" indicates that it was found in very small amounts.

	Molluscs					Polychaetes				
Prey	Mean	± SD	Min	Max	Est	Mean	± SD	Min	Max	Est
Large cod										
Small cod										
Large Green. halibut										
Small Green. halibut										
American plaice										
Flounders										
Skates										
Redfish										
Large demersals										
Small demersals										
Capelin										
Sand lance										
Arctic cod										
Large pelagics										
Pisci. small pelagics										
Plank. small pelagics										
Shrimp										
Large crustacea										
Echinoderms										
Molluscs										
Polychaetes						13.4	16.5	1.8	25.1	9.2
Other bent. inver.										
Large zooplankton										
Small zooplankton										
Phytoplankton	5.0	7.1	0.0	10.0	9.2	43.3	8.2	37.5	49.1	48.2
Detritus	95.0	7.1	90.0	100.0	90.8	43.3	8.2	37.5	49.1	42.6
Total	100.0		90.0	110.0	100.0	100.0		76.7	123.3	100.0
TRN	2					3				

Large zooplankton

Background

Species representing this group are greater than 5 mm in length and include euphausiids, chaetognaths, hyperiid amphipods, jellyfish (cnidarians and ctenophores), mysids, tunicates, and ichthyoplankton. This group contains herbivorous (some euphausiid species), omnivorous (most euphausiids, hyperid amphipods, mysiids, and large tunicates), and carnivorous (chaetognaths and jellyfish) species.

Catch

There was no commercial fishery for species in this group during the 1985–87 period in the northern Gulf.

Biomass

Biomass was calculated from euphausiid data gathered in 1973 off Anticosti Island and in the northwestern Gulf of St. Lawrence (Sameoto and Jarosynski 1973). In the absence of more current information, it was assumed that euphausiid biomass was similar during the 1985–87 period. We used this value as a guesstimate for large zooplankton group. This gives a biomass estimate of 9.643 t km^{-2} (SD = 14.482 t km^{-2}) or 1,001,007 t for the study area.

Production

The euphausiid P/B estimate was obtained from several different sources. These sources included P/B ratios of 4.000 yr^{-1} for the Gulf of St. Lawrence (Berkes 1977), 2.750 to 3.840 yr^{-1} for the North Sea and American coastal waters (Lindley 1980; Lindley 1982), and 1.600 yr^{-1} for the northeast Atlantic off the west coast of Ireland (Mauchline 1985). Production could thus range between 15.428 and 38.570 t km^{-2} yr^{-1}, corresponding to an annual production of 29.289 ± 10.646 t km^{-2} yr^{-1}. The inverse solution estimated a production of 38.379 t km^{-2} yr^{-1}, representing a P/B of 3.980 yr^{-1}.

Consumption

Consumption was estimated from data on euphausiids in the Gulf of St. Lawrence (Sameoto 1976). This produced a consumption range between 46.370 and 207.938 t km^{-2} yr^{-1}. Based on the mean production (29.289 t km^{-2} yr^{-1}) for large zooplankton and the minimum and maximum GE limits (10–30%), we obtained two other consumption values of 97.630 and 292.891 t km^{-2} yr^{-1}. The resulting lower and upper consumption limits were 46.370 and 292.891 t km^{-2} yr^{-1}, corresponding to a mean consumption of 169.631 ± 110.686 t km^{-2} yr^{-1}. The inverse solution estimated a consumption of 229.945 t km^{-2} yr^{-1} for large zooplankton, representing a Q/B ratio of 23.847 yr^{-1}.

Diet composition

No diet information was available for these species in the northern Gulf of St. Lawrence. In other areas, euphausiids feed on detritus, phytoplankton, chaetognaths, amphipods, and crustaceans (copepods) (Mauchline 1980). Chaetognaths and jellyfish eat copepods (Sullivan 1980; Smayda 1993). The relative proportions of these prey in the large zooplankton diet were 5% large zooplankton, 43% small zooplankton, 37% phytoplankton, and 20% detritus (Bundy et al. 2000) (Table 16).

Table 16. Diet composition of large zooplankton used in modelling. Est: diet estimates by the inverse model; TRN: number of trophic relations; SD: standard deviation. All values are percentages except TRN. Empty cells indicate that a prey item was never found whereas "0.0" indicates that it was found in very small amounts.

	Large zooplankton (> 5 mm)				
Prey	Mean	± SD	Min	Max	Est
Large cod					
Small cod					
Large Green. halibut					
Small Green. halibut					
American plaice					
Flounders					
Skates					
Redfish					
Large demersals					
Small demersals					
Capelin					
Sand lance					
Arctic cod					
Large pelagics					
Pisci. small pelagics					
Plank. small pelagics					
Shrimp					
Large crustacea					
Echinoderms					
Molluscs					
Polychaetes					
Other bent. inver.					
Large zooplankton	5.0	5.0	0.0	10.0	0.0
Small zooplankton	43.0	7.1	38.0	48.0	39.2
Phytoplankton	37.0	30.7	6.3	67.7	48.9
Detritus	15.0	7.1	10.0	20.0	11.9
Total	100.0		54.3	145.7	100.0
TRN	4				

Small zooplankton

Background

The small zooplankton includes zooplankton less than or equal to 5 mm in length. Copepods, mainly *Calanus finmarchicus* and *Oithona similis*, are the most numerous small plankton. Also included in the small zooplankton category are meroplankton and tunicates < 5 mm, which are generally underestimated by sampling gear (Strong 1981). The most recent comprehensive source of information on the small zooplankton in the northern Gulf of St. Lawrence was a study carried out from July 1992 to June 1994 during the Canadian Joint Global Ocean Flux Study (JGOFS) program (Roy et al. 2000). Calanoid copepods accounted for 20 to 70% of the numerical abundance of all zooplankton species present, with *Calanus finmarchicus/glacialis* (not distinguished in the counts) and *C. hyperboreus* generally dominant among the mid-sized organisms (i.e., those retained by the 500 μm mesh). The greatest numbers of the *Calanus* spp. were observed at the deeper Laurentian trough stations. The small cyclopoid copepod *Oithona similis* was also very abundant, ranging from 20 to 70% of the numerical abundance of all species.

Catch

None.

Biomass

Data from day and night hauls were averaged over the top 150 m at three stations (Anticosti Gyre, Anticosti Channel, and Cabot Strait stations) for each season (Savenkoff et al. 2000). The mean biomass for the entire area was 3,534 ± 1,814 mg C m^{-2} for all the small zooplankton. The range was wide and we assumed that it should account for the heterotrophic protozoan (flagellates, dinoflagellates, and ciliates) biomass (1,177 ± 580 mg C m^{-2}). Using a conversion factor of 10 g wet mass = 1g C (Christensen and Pauly 1992b), we obtained 35.336 ± 18.137 t wet mass km^{-2}. The minimum–maximum range was 17.199–53.473 t wet mass km^{-2}. Based on de Lafontaine et al. (1991, see their Fig. 7), another minimum–maximum biomass range was estimated as 1–24 g dry mass m^{-2} or 5.000–120.000 t wet mass km^{-2} yr^{-1} for small zooplankton. Biomass could thus range between 5.000 and 120.000 t km^{-2}, corresponding to a mean value of 50.000 ± 81.317 t km^{-2}.

Production

Production (94.76 mg C m^{-2} d^{-1} or 345.886 t wet mass km^{-2} yr^{-1}) was estimated from Vézina et al. (2000). However, de Lafontaine et al. (1991) estimated 1 g C m^{-2} mo^{-1} (or 120.00 t wet mass km^{-2} yr^{-1}) for secondary production of copepod-sized organisms. Production could thus range between 120.000 and 345.886 t km^{-2} yr^{-1}, corresponding to an annual production of 232.943 ± 159.725 t km^{-2} yr^{-1}. The inverse solution estimated a production of 338.056 t km^{-2} yr^{-1}, representing a P/B of 6.761 yr^{-1}.

Consumption

Vézina et al. (2000) estimated a minimum consumption value (120.04 mg C m^{-2} d^{-1} or 438.135 t wet mass km^{-2} yr^{-1}) for the summer and fall periods and a maximum (425.94 mg C m^{-2} d^{-1} or 1,554.666 t wet mass km^{-2} yr^{-1}) value for the winter and spring periods. These lower and upper limits, along with the corresponding mean (272.99 ± 216.30 mg C m^{-2} d^{-1} or 996.401 ± 789.507 t wet mass km^{-2} yr^{-1}) were used. The inverse solution estimated a consumption of 1,296.281 t km^{-2} yr^{-1}, representing a Q/B of 25.926 yr^{-1}.

Diet composition

The small zooplankton feed on both autotrophic and heterotrophic microplankton. However, heterotrophic microplankton (heterotrophic dinoflagellates, ciliates, and small metazoans) were included in the small zooplankton group here. Moreover, there is ample empirical evidence that mesozooplankton is omnivorous (Stoecker and Capuzzo 1990; Ohman and Runge 1994; Vézina et al. 2000). Small zooplankton, phytoplankton, and detritus were thus assumed to be potentially accessible to small zooplankton (Table 17).

Table 17. Diet composition of small zooplankton used in modelling. Est: diet estimates by the inverse model; TRN: number of trophic relations; SD: standard deviation. All values are percentages except TRN. Empty cells indicate that a prey item was never found whereas "0.0" indicates that it was found in very small amounts.

	Small zooplankton (> 5 mm)				
Prey	Mean	± SD	Min	Max	Est
Large cod					
Small cod					
Large Green. halibut					
Small Green. halibut					
American plaice					
Flounders					
Skates					
Redfish					
Large demersals					
Small demersals					
Capelin					
Sand lance					
Arctic cod					
Large pelagics					
Pisci. small pelagics					
Plank. small pelagics					
Shrimp					
Large crustacea					
Echinoderms					
Molluscs					
Polychaetes					
Other bent. inver.					
Large zooplankton					
Small zooplankton	12.5	12.5	9.3	26.9	9.5
Phytoplankton	54.1	47.6	0.0	67.3	64.5
Detritus	33.4	35.2	23.4	73.1	26.0
Total	100.0		32.7	167.3	100.0
TRN	3				

Phytoplankton

Background

Most information on phytoplankton in the northern Gulf of St. Lawrence was derived from a study carried out from July 1992 to June 1994 during the Canadian Joint Global Ocean Flux

Study (JGOFS) program (Savenkoff et al. 2000). These authors described the seasonal changes in photosynthetic production, respiration, sinking flux of organic carbon, and food web structure in the Gulf of St. Lawrence over a two-year period.

Diatoms were the most abundant phytoplankton in terms of both cell numbers and biovolumes during spring and winter. A mixture of autotrophic and mixotrophic organisms including Cryptophytes, diatoms, dinoflagellates, Prasinophytes, and mixotrophic *Stombidium* spp. (in the Spirotrichea) dominated during summer and fall. Prymnesiophytes were important in terms of cell numbers during spring and winter. The diatoms were dominated by *Chaetoceros affinis*, *Chaetoceros* spp., *Leptocylindrus minimus*, and *Thalassiiosira nordenskioldii* during winter and by *Thalassiiosira* spp. (*T. punctigera*, *T. nordenskioldii*, *T. pacifica*, and *T. bioculata*) and *Fragilariopsis* spp. (*F. oceanica* and *F. cylindrus*) during spring. During summer, the importance of diatoms in the phytoplankton composition was lower, with the majority observed being smaller centric diatoms such as *Minidiscus* sp., *Chaetoceros minimus*, and occasionally larger *Coscinodiscus* sp.

Phytoplankton biomass and production are the only two parameters required for modelling. There is no harvest, and since they are autotrophs, there is no consumption and no diet.

Biomass

Phytoplankton biomass is measured as chlorophyll *a* biomass. Mean annual chlorophyll *a* biomass (47 ± 33 mg CHL m^{-2}) was estimated as the mean of the seasonal biomass averages integrated over the euphotic zone (defined as the depth of 1% surface incident radiation) (Savenkoff et al. 2000). To facilitate comparisons with other studies in the Gulf of St. Lawrence, phytoplankton carbon biomass was estimated by converting measured chlorophyll *a* concentrations (CHL) to carbon (C) using a C/CHL ratio of 50 (Rivkin et al. 1996; Savenkoff et al. 2000).

The mean biomass for the entire area was 2.3 ± 1.6 g C m^{-2} or 23.411 ± 16.474 t km^{-2}, using a conversion factor of 10 g wet mass = 1g C (Christensen and Pauly 1992b). The minimum–maximum range was 5.009–45.452 t km^{-2}.

Primary Production

Primary productivity was estimated from the same data sources as described above. A value of 674 ± 301 mg C m^{-2} d^{-1} was estimated over the euphotic zone (Savenkoff et al. 2000). This represented 245.9 ± 109.9 g C m^{-2} yr^{-1} or 2,458.998 ± 1,098.820 t km^{-2} yr^{-1}. The minimum–maximum range was 1,360.178-3,557.818 t wet mass km^{-2} yr^{-1}. The inverse solution estimated a production of 1,559.255 t km^{-2} yr^{-1}, representing a P/B of 66.603 yr^{-1}.

Detritus

Biomass

The detritus mass was estimated using an empirical relationship derived by Pauly et al. (1993) that relates detritus biomass to primary productivity and euphotic depth.

$$\log_{10} D = -2.41 + 0.954 \log_{10} PP + 0.863 \log_{10} E \qquad (8)$$

where D is the standing stock of detritus (g C m^{-2}), PP is primary productivity (g C m^{-2} yr^{-1}), and E is the euphotic depth (m).

The annual value for primary production was 245.9 ± 109.9 g C m^{-2} yr^{-1}. The euphotic depth is estimated from Savenkoff et al. (2000) as 28.2 ± 5.9 m. The primary production estimate and euphotic depth were substituted into equation 10, giving a range of detritus biomass estimates from 6.2 to 22.2 g C m^{-2}, or 61.630 to 222.058 t km^{-2}, using a conversion factor of 10 g wet mass = 1g C (Christensen and Pauly 1992b). This resulted in a mean detritus biomass of 132.608 ± 113.440 t km^{-2}.

Here, bacteria was considered part of the detritus compartment. Detritus estimates had a wide range, and it was assumed that this range should allow for the bacteria biomass (bacterial biomass: 184 ± 40 mg C m^{-2} or 1.8 ± 0.4 t km^{-2}; Savenkoff et al. 2000).

Respiration

Detritus is usually assumed not to respire. However, as bacteria were considered part of the detritus in this study, there would be respiration involved. Based on Savenkoff et al. (2000), we estimated a planktonic respiration (organisms < 200 μm including bacteria) close to 162 ± 33 mg C m^{-2} d^{-1} and 383 ± 152 mg C m^{-2} d^{-1} for the winter–spring and summer–fall periods, respectively, in the euphotic zone of the northern Gulf of St. Lawrence. Vézina et al. (2000) applied inverse modelling to the data collected from July 1992 to June 1994 to estimate trophic flows in the planktonic food web and to calculate export fluxes consistent with mass balance. These authors estimated that the phytoplankton respiration represented 8 and 20% of the primary production for the winter–spring and summer–fall periods, respectively (R_{PHY} = 80 ± 41 mg C m^{-2} d^{-1} for winter–spring and 70 ± 64 mg C m^{-2} d^{-1} for summer–fall). By subtracting, we could estimate a detrital (or bacterial) respiration of 82 ± 53 mg C m^{-2} d^{-1} and 313 ± 165 mg C m^{-2} d^{-1} for the winter–spring and summer–fall periods, respectively. This represented 198 ± 86 mg C m^{-2} d^{-1} or 72 ± 32 g C m^{-2} yr^{-1} for the euphotic zone.

Based on the data collected from July 1992 to June 1994 at three stations located in the Laurentian Channel, Savenkoff et al. (1996) estimated a bacterial respiration of 44 ± 9 mg C m^{-2} d^{-1} or 16 ± 28 g C m^{-2} yr^{-1} in the aphotic layer (up to 300 m depth). By adding bacterial respiration values estimated in the euphotic and aphotic layers, a total detrital respiration could be estimated as 88.3 ± 42.4 g C m^{-2} yr^{-1} or 882.961 ± 423.748 t km^{-2} yr^{-1} (range: 459.213-1,306.710 t km^{-2} yr^{-1}). The inverse solution estimated a detrital respiration of 616.125 t km^{-2} yr^{-1}.

Export

The fraction of the organic carbon that is not returned to the water column but is buried and preserved within the sediment represents the export of detritus. Silverberg et al. (2000) estimated a burial flux of particulate organic carbon between 0.46 and 0.53 mol C m^{-2} yr^{-1} at the Anticosti Gyre and Cabot Strait stations, respectively. This represented a detrital export close to 5.9 ± 0.6 g C m^{-2} yr^{-1} or $5.94 \times 10^1 \pm 0.59 \times 10^1$ t km^{-2} yr^{-1}. The inverse solution estimated a detrital export of 5.62×10^1 t km^{-2} yr^{-1}.

Data synthesis

Data about biomass, export (here equal to commercial catch), production, and consumption are summarized in Tables 18 and 19.

Table 18. Observed biomass and export for each group used as input parameters for modelling for the 1985–1987 period in the northern Gulf of St. Lawrence. SD: standard deviation, Min: minimum, Max: maximum. Est: value estimates by the inverse modelling.

	Biomass (t wet mass km^{-2})				Exports (t km^{-2} yr^{-1})[a]				
Group	Value	± SD	Min	Max	Value	± SD	Min	Max	Est.
Cetaceans	0.137	0.090[b]			3.75×10^{-4}	2.09×10^{-5}	3.60×10^{-4}	3.90×10^{-4}	3.74×10^{-4}
Harp seals	0.085	0.005	0.080	0.089	5.82×10^{-3}	1.63×10^{-3}	4.20×10^{-3}	7.45×10^{-3}	4.49×10^{-3}
Hooded seals	0.003	0.000	0.003	0.004	1.85×10^{-4}	2.60×10^{-4}	0	3.68×10^{-4}	1.33×10^{-4}
Grey seals	0.018	0.001	0.017	0.019	6.41×10^{-4}	4.02×10^{-4}	2.34×10^{-4}	1.04×10^{-3}	5.62×10^{-4}
Harbour seals	0.003	0.000	0.002	0.003					
Seabirds	0.004	0.003[b]			3.35×10^{-4}	1.54×10^{-4}[c]			3.40×10^{-4}
Large cod	3.929	0.813	2.990	4.402	7.63×10^{-1}	1.09×10^{-1}	6.41×10^{-1}	8.50×10^{-1}	7.55×10^{-1}
Small cod	1.643	0.470	1.115	2.017	8.18×10^{-4}	6.65×10^{-4}	6.50×10^{-5}	1.33×10^{-3}	8.55×10^{-4}
Large Green. halibut	0.272	0.108	0.076	0.566	2.54×10^{-2}	1.74×10^{-2}	1.03×10^{-2}	4.44×10^{-2}	2.65×10^{-2}
Small Green. halibut	0.287	0.130	0.058	0.578					
Amer. plaice	0.666	0.405	0.218	1.744	2.04×10^{-2}	2.50×10^{-3}	1.77×10^{-2}	2.26×10^{-2}	2.10×10^{-2}
Flounders	0.350	0.320	0.000	2.126	7.48×10^{-3}	1.08×10^{-3}	6.71×10^{-3}	8.71×10^{-3}	7.46×10^{-3}
Skates	0.167	0.069	0.100	0.252	6.42×10^{-5}	7.36×10^{-5}	0	1.44×10^{-4}	6.84×10^{-5}
Redfish	12.149	2.461	2.975	26.915	2.65×10^{-1}	2.56×10^{-2}	2.36×10^{-1}	2.85×10^{-1}	2.64×10^{-1}
Large demersals	0.972	0.171	0.646	1.390	9.26×10^{-3}	1.44×10^{-3}	8.11×10^{-3}	1.09×10^{-2}	9.21×10^{-3}
Small demersals	1.343	1.835	0.045	2.640					
Capelin	16.674	23.481	0.070	33.277	2.32×10^{-2}	1.37×10^{-2}	8.74×10^{-3}	3.61×10^{-2}	2.45×10^{-2}
Sand lance	2.398	0.416	2.103	2.692					

Table 18. Cont.

Group	Biomass (t wet mass km^{-2})				Exports (t km^{-2} yr^{-1})[a]				
	Value	± SD	Min	Max	Value	± SD	Min	Max	Est.
Arctic cod	0.024	0.034	0.000	0.048					
Large pelagics	0.059	0.028	0.024	0.085	2.49×10^{-3}	2.22×10^{-3}	1.06×10^{-3}	5.05×10^{-3}	2.66×10^{-3}
Pisci. small pel. feeders	2.456	0.851	1.673	3.362	1.25×10^{-2}	1.71×10^{-2}	1.65×10^{-3}	3.22×10^{-2}	1.38×10^{-2}
Plank. small pel feeders	2.534	0.070	2.434	2.656	1.76×10^{-1}	3.46×10^{-2}	1.44×10^{-1}	2.12×10^{-1}	1.77×10^{-1}
Shrimp	0.830	0.561	0.578	1.083	9.40×10^{-2}	1.49×10^{-2}	8.29×10^{-2}	1.11×10^{-1}	9.07×10^{-2}
Large crustaceans	0.862	0.204	0.369	2.142	4.39×10^{-2}	3.33×10^{-3}	4.02×10^{-2}	4.67×10^{-2}	4.41×10^{-2}
Echinoderms	112.300	73.792[b]							
Molluscs	42.100	27.664[b]			3.34×10^{-2}	4.10×10^{-3}	3.08×10^{-2}	3.81×10^{-2}	3.34×10^{-2}
Polychaetes	10.500	6.900[b]							
Other benthic invertebrates	7.800	5.125[b]							
Large zooplankton	9.643	14.482	0.010	63.000					
Small zooplankton	50.000	81.317	5.000	120.000					
Phytoplankton	23.411	16.474	5.009	45.452					
Detritus	132.608	113.440	61.630	222.058	5.94×10^{1}	0.59×10^{1}	5.35×10^{1}	6.53×10^{1}	5.62×10^{1}

[a]: Export is the sum of the catch and the net migration (emigration out of the system, food intake of predators that are not part of the system, etc.; this term is assumed here to be equal to 0). For detritus, export was loss of detritus buried as sediment.

[b]: calculated as $B_X{*}CV(B_Y)_{mean}$ with $CV(B_Y)_{mean} = 66\%$, the average of all coefficients of variation for observed biomass.

[c]: calculated as $Exp_X{*}CV(Exp_Y)_{mean}$ with $CV(Exp_Y)_{mean} = 46\%$, the average of all coefficients of variation for observed export.

Table 19. Observed production and consumption used as input parameters for modelling for the 1985–1987 period in the northern Gulf of St. Lawrence. SD: standard deviation, Min: minimum, Max: maximum. Est: value estimates by the inverse modelling.

	Production ($t\ km^{-2}\ yr^{-1}$)					Consumption ($t\ km^{-2}\ yr^{-1}$)				
Group	Value	± SD	Min	Max	Est.	Value	± SD	Min	Max	Est.
Cetaceans	0.010	0.002	0.008	0.011	0.009	0.896	0.102	0.824	0.969	0.960
Harp seals	0.007	0.004	0.004	0.010	0.006	0.511	0.228	0.350	0.672	0.609
Hooded seals	0.0003	0.0001	0.0002	0.0004	0.0003	0.038	0.009	0.032	0.044	0.034
Grey seals	0.0010	0.0007	0.0005	0.0015	0.0010	0.064	0.054	0.026	0.103	0.100
Harbour seals	0.0001	0.0001	0.0001	0.0002	0.0001	0.012	0.004	0.010	0.015	0.014
Seabirds	0.0011	0.0010[a]			0.0012	0.309	0.280	0.111	0.507	0.163
Large cod	2.312	1.079	1.549	3.075	1.649	14.330	8.339	5.540	23.120	7.580
Small cod	0.986	0.383	0.669	1.210	0.747	10.457	6.595	3.286	17.628	3.712
Large Green. halibut	0.050	0.055	0.017	0.095	0.063	0.386	0.147	0.272	0.500	0.313
Small Green. halibut	0.057	0.073	0.012	0.116	0.087	0.780	0.448	0.287	1.272	0.467
Amer. plaice	0.167	0.241	0.066	0.406	0.304	1.890	1.150	0.666	3.114	1.953
Flounders	0.077	0.302	0.007	0.434	0.177	0.595	0.319	0.350	0.840	0.678
Skates	0.036	0.023	0.021	0.054	0.050	0.322	0.153	0.167	0.477	0.277
Redfish	1.783	2.151	0.608	3.650	2.411	54.490	41.821	12.149	96.830	13.123
Large demersals	0.106	0.055	0.073	0.150	0.139	1.992	1.376	0.972	3.013	1.133
Small demersals	0.440	0.610	0.009	0.871	0.614	3.817	3.325	1.467	6.168	2.257
Capelin	10.016	14.105	0.042	19.989	13.337	132.389	117.322	0.559	264.220	57.076
Sand lance	2.757	2.562[a]			2.930	18.381	12.997	9.190	27.571	14.693

Table 19. Cont.

	Production ($t\ km^{-2}\ yr^{-1}$)					Consumption ($t\ km^{-2}\ yr^{-1}$)				
Group	Value	± SD	Min	Max	Est.	Value	± SD	Min	Max	Est.
Arctic cod	0.009	0.013	0.000	0.019	0.016	0.063	0.045	0.032	0.095	0.072
Large pelagics	0.008	0.007	0.003	0.014	0.012	0.366	0.292	0.059	0.672	0.079
Pisci. small pel. feeders	0.481	0.172	0.335	0.676	0.648	8.626	5.870	2.456	14.795	3.305
Plank. small pel feeders	0.683	0.080	0.630	0.744	0.744	18.610	14.809	2.534	34.686	3.355
Shrimp	1.204	0.517	0.838	1.570	1.449	8.028	5.676	4.014	12.041	5.970
Large crustaceans	0.216	0.255	0.114	0.475	0.289	1.442	0.609	0.721	2.163	1.224
Echinoderms	33.667	38.755	0.108	70.108	36.257	243.147	185.156	112.222	374.072	190.634
Molluscs	22.949	34.282	0.600	82.121	39.278	165.744	126.214	76.497	254.991	171.020
Polychaetes	16.680	24.487	0.206	74.564	26.750	120.468	91.737	55.601	185.336	113.794
Other benthic invertebrates	9.173	7.631	0.517	15.677	9.172	66.252	50.451	30.578	101.926	48.485
Large zooplankton	29.289	10.646	15.428	38.570	38.379	169.631	110.686	46.370	292.891	229.945
Small zooplankton	232.943	159.725	120.000	345.886	338.056	996.401	789.507	438.135	1554.666	1296.281
Phytoplankton	2458.998	1098.820	1360.178	3557.818	1559.255					
Detritus										

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[a]: Calculated as $P_X{*}CV(P_Y)_{mean}$ with $CV(P_Y)_{mean} = 93\%$, the average of all coefficients of variation for observed production.

DISCUSSION

The CDEENA project is focussing on the comparison of different ecosystems (northern and southern Gulf of St. Lawrence, Newfoundland–Labrador Shelf, Scotian Shelf) for different time periods, i.e., the pre-collapse period (1985–1987) and the post-collapse period (1994–1996) in the groundfish stocks. The time periods were determined after the analysis of biomass fluctuations for the key species of the system (i.e., seals and cod) in the pre- and the post-collapse periods. These time periods have been chosen in order to have available and stable information on biomass (Jarre et al. 1991). The present models of the northern Gulf of St. Lawrence have been done for the pre-collapse period.

The quality of the input data was variable (Figure 2). For catch estimates (export), values were quite good because catch data for 4RS were available for several years. They often provided some measure of variability; however, other factors such as weather or market forces could also affect catches (Figure 2A). The accuracy of the data depends on the quality of the assessments. For example, one weakness in these data is the lack of information on discarding or misreporting (unaccounted fishing mortality). In some cases, non-declared catches could be substantial (Fréchet 1991; Hurtubise et al. 1992; Palmer and Sinclair 1997) and as a result, the catch data may only represent minimum values. These shortcomings in catch statistics have been identified in other studies attempting to develop ecosystem models and represent an important obstacle to improving management and sustainable development of fisheries resources (Silvestre et al. 1993; Bundy et al. 2000). Uncertainty also occurs for the catch estimate of small Greenland halibut, which was assumed to be null. However, this could be biased since there seems to be a large by-catch of this species in the shrimp fishery (Orr et al. 2000) even though no information is available for the northern Gulf area. However, the shrimp fishery in 1985–1987 was not as important as in 1997-1999 when the by-catch study by Orr et al. (2000) was done.

Local data were available to obtain estimates of biomass (Figure 2B). Good estimates of biomass for harvested species, harp and grey seals are available, but information on hooded seal and harbour seal biomass are very limited, particularly for the mid-1980s. Also, in many other cases, it was necessary to use empirical data from other areas and/or time frames (e.g., capelin, sand lance, Arctic cod) or less specific information (e.g., small cod, pelagic feeders, benthic invertebrates). For example, a large proportion of small cod resides in the inshore and gradually moves offshore at ages of 1 to 3 years (M. Castonguay, personal communication). Inshore areas are not covered as thoroughly and fishing techniques during research surveys are not adapted to assessing small cod abundance, particularly their winter distribution. Likewise, mackerel biomass was assumed to be uniformly distributed throughout the area and surface proportions were used to quantify biomass in 4RS. However, it is primarily the larger mackerel that move into 4RS, with the smallest mackerel staying in 4T (F. Grégoire, personal communication). Therefore, the mackerel biomass in the area may be overestimated. For fish, the biomass estimates are calculated from sequential population analysis or a scientific trawl survey that provides only an index of the real biomass in the ecosystem. We attempted to adjust for this by converting the trawlable biomass estimates to catchability-adjusted biomass based on the catchability coefficients estimated by Harley and Myers (2001).

Very little is known about fish and invertebrate production in the Gulf of St. Lawrence (Figure 2C). For fish, the majority of the production estimates were obtained assuming that production or total mortality is equivalent to biomass multiplied by natural mortality plus the catch in the absence of information on total mortality ($Z = P/B$). Unfortunately, we have few measures of natural mortality. In many cases we have assumed that natural mortality is equal to a fixed value (0.2) to get a preliminary production estimate that can then vary over a wide range. Little is known about the variability of this parameter. In a recent study on natural mortality of cod in the adjacent NAFO Division 4T, it was shown that the traditionally used value of $M = 0.2$ was too low for the 1990s period and that a more appropriate estimate was $M = 0.4$ for 1993–1996 (Sinclair 2001). The same study also suggests that an increase in natural mortality occurred in the early 1980s. Therefore, our estimate of $M = 0.2$ for the end of the 1980s may underestimate natural mortality for a part of our modelling period. This means that we may also underestimate the total mortality (Z) and the P/B ratio.

Consumption is the variable for which values are the most uncertain. Without any other information, consumption or the Q/B value was usually taken from diet studies coming from other regions and covering other time periods (Figure 2D). This represents a considerable weakness in the model construction. Similar problems dealing with production and consumption estimates have been encountered and discussed for other ecosystem models, such as the Grand Banks of Newfoundland (Bundy et al. 2000), the South China Sea (Silvestre et al. 1993), and Lake Malawi (South Africa) (Degnbol 1993). More efforts are needed to obtain more information on fish and invertebrate production and consumption, to increase the quality of ecosystem models.

For large or commercially exploited species such as seals, large cod, large Greenland halibut, and redfish, we can consider that the empirical estimates are quite good because they are based on information obtained in the study area and during the period of interest. A considerable effort has been expended to obtain biomass, diet, and catch data for these species, and even for year- or size-classes within these species. On the other hand, consumption and production estimates for some of these species (e.g., cod, Greenland halibut, and redfish) remain unknown for the 4RS area.

Further uncertainties with diet data resulted from assuming that the diet for a key species is representative of the functional group to which it belonged, or attributing the proportion of "unidentified" in stomach content analysis in proportion to the different identified groups in the stomachs.

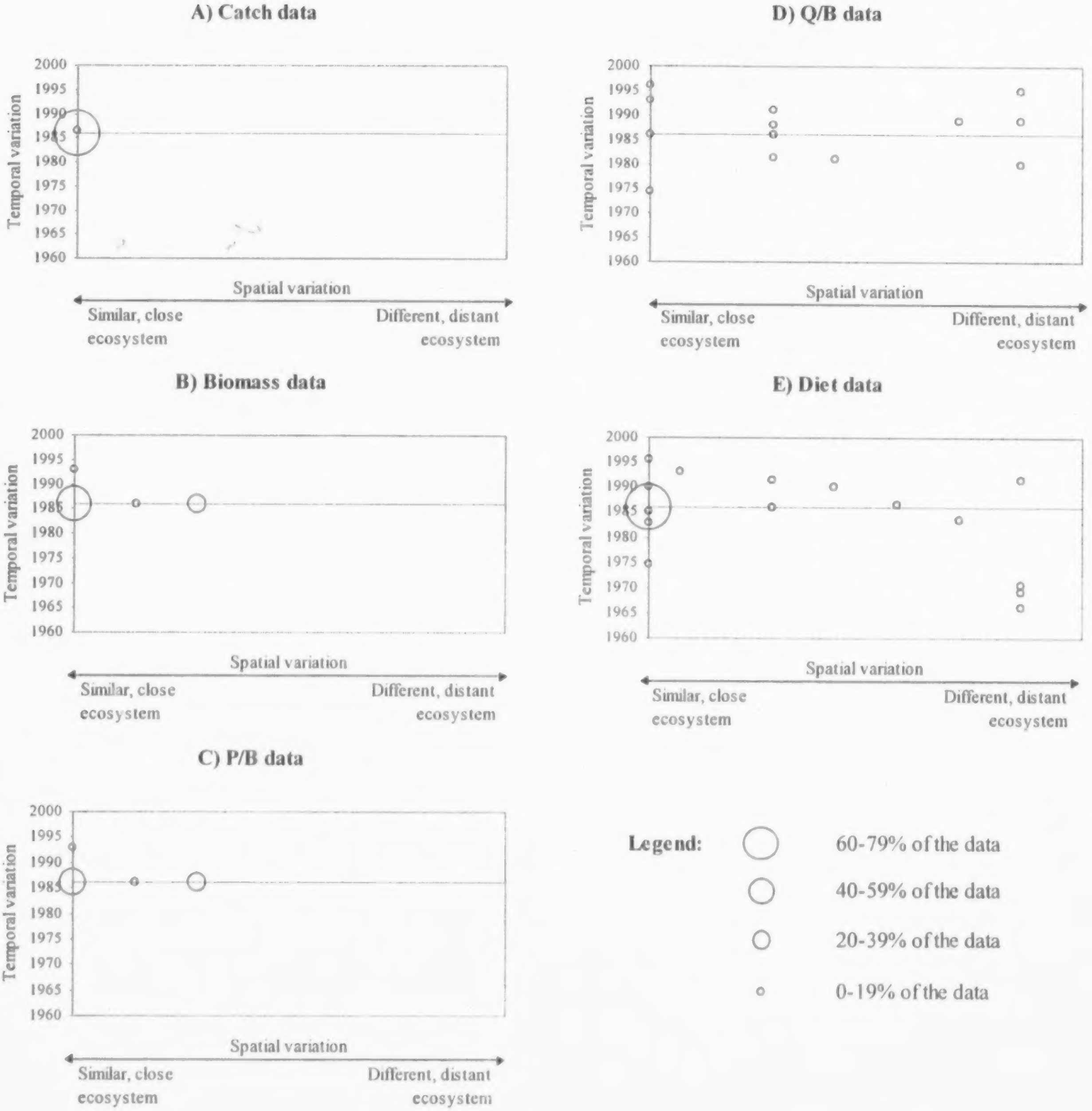

Figure 2. Geographical and temporal variation in the sources of information used to estimate values entered in the 4RS Ecopath model.

All the forage species of the ecosystem are described in this model with very uncertain values. Furthermore, these species represent an important part of the food chain. Consequently, effort should be expended to examine the distribution and biomass of small commercially important species and, perhaps more importantly, to obtain information on small forage species for which we have little information.

Strengths and weaknesses of the modelling efforts

The synthesis of existing ecosystem information is designed to enable a whole-system view using parameters that are basic to understanding populations and the ecosystem (Okey and Pauly 1999). Unfortunately, the model is not a perfect representation of the reality. The uncertainties remaining in the understanding of the ecosystem may occur because no data exist, because the confidence limits are too large, because of an inappropriate aggregation of species within one ecological box, because the ecotrophic efficiency is unlikely, or from unknown mechanisms occurring in the ecosystem (Ruesink 1998). Indeed, the only mechanism used to represent interactions is direct consumption. It ignores the fact that consumers often do more than skim production off their prey; consumers can shift diet composition to species with lower productivity and alter the P/B ratio of the group (Ruesink 1998). However, these errors are important only if the questions addressed by the model are drawn on aspects of the model that are fundamentally wrong. For instance, it would be imprudent to try to set fisheries quotas with this kind of model. The structure of the model provides an overall view of the ecosystem and reveals the uncertainties that could be examined in future studies. Consequently, one of the most important questions that can be asked of Ecopath models is: in which portion of the food web are the dynamics most uncertain? (Ruesink 1998). Addressing these uncertainties is important because it could help to identify if current fishing practices or environmental conditions are placing undue stress on one ecosystem component that could have longer term impacts on other fisheries or other ecosystem components.

A common problem in ecosystem modelling is that less information is available for the lower trophic levels (Moreau et al. 1993; Walline et al. 1993; Lin et al. 1999). These recurrent gaps generally force modellers to rely heavily on the literature and arbitrary assumptions to construct the models (Moreau et al. 1993). This emphasizes the need for an increased research effort into the biomass, production, consumption, and diet of the various species of the ecosystem. Some progress is still needed in understanding and refining the structure of ecosystem models in the Gulf of St. Lawrence as well as in other areas of the world.

Different tools are used for ecosystem modelling in the northwest Atlantic, each with its strengths and its weaknesses. Inverse models provide a powerful tool to estimate ecosystem flows using sparse observations and straightforward mass balance and constraints. The structure of the model provides an overall view of all the data of the ecosystem and underlines the uncertainties that could be filled with future studies. The use of upper and lower limits to constrain the majority of input values (production, consumption, export, and diet composition) and the choice of row and column weights make inverse modelling a flexible tool to quantify mass-balanced flow diagrams and trophic transfer efficiencies that are internally consistent. Given sufficient data, they enable a rigorous consistency of the different information used to quantify the flow diagram and allow guesstimates of some fluxes that are inaccessible for measurements (Gaedke 1995).

Since the number of flows to be solved exceeded the number of independent mass balance relations, the solutions are not unique. Also, since our empirical databases and scientific understanding of ecological processes will always be incomplete, Whipple et al. (2000) suggested the use of multiple model configurations to allow for an explicit implementation and assessment of this uncertainty. Indeed, where one modelling approach compromises or simplifies portions of the system, another may provide a realistic and precise representation of the same parts of the system. In this study, different approaches based on random perturbations and sensitivity tests were thus compared to provide an overall view of the ecosystem, to identify general robust patterns, and to show where are the uncertainties in the food web.

CONCLUSION

This work represents the first ecosystem model for the northern Gulf of St. Lawrence and is the result of a huge effort to assemble data on the biological characteristics of species occurring in 4RS. Even though most of the data are good estimates for the 4RS ecosystem during the 1985–1987 period, some other input values are rough estimates only, meaning that these values are assembled from different literature sources and not from independently measured parameters. Some errors in parameter estimates could significantly alter the system's biomass budget, especially for the most important species of the ecosystem, or produce a totally different balanced solution. Although the top predators appear to be reasonably represented, there is an evident lack of data on particular key species such as the capelin, Arctic cod, and other prey species. This illustrates the need for further work to improve the input parameters in order to improve the quality of future modelling efforts. In conclusion, this model enabled us to bring together wide ranging data concerning the northern Gulf of St. Lawrence ecosystem. By doing so, it allowed us to focus attention on uncertainties in our knowledge on the ecosystem's structure and to identify where research efforts should be directed if we are to gain a better understanding of this ecosystem.

ACKNOWLEDGEMENTS

This study was carried out as a contribution to the Canadian CDEENA (Comparative Dynamics of Exploited Ecosystems in the Northwest Atlantic) program with financial support from Fisheries and Oceans Canada (Science Strategic Funds). We are grateful to colleagues who made data available for this report. Gratitude is extended to L. Devine and S. Guénette for their comments and reviews of the manuscript.

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